

The utility of fossil data in phylogenetic analyses: a likelihood example using Ordovician-Silurian species of the Lophospiroidea (Gastropoda: Murchisoniina)

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Abstract: Gastropods have a dense fossil record dating back to the Late Cambrian. Intuitively, this would appear to aid phylogenetic reconstructions. However, workers question both whether gastropod shell characters are phylogenetically informative and whether stratigraphic data can be used to test phylogenetic hypotheses. Both questions are addressed with an analysis of 82 species of the Lophospiroidea (= Lophospiridae + Trochonematidae) from the Ordovician and Silurian. Compatibility analyses of 95 shell characters shows that characters are far more compatible than one would expect from homoplasy-saturated data. However, compatibility among the 73 characters that vary among the earliest lophospirids decreases over time, which suggests that later species introduced homoplasy. Simulations using 95 characters and sampling similar to that observed for lophospirids show that parsimony performs poorly relative to methods that incorporate stratigraphic data such as stratocladistics. An alternative approach is used here. The first step is to estimate the likelihood of a hypothesized tree given observed character congruence (*i. e.* parsimony length) using simulations. The second step uses two different statistical tests to estimate the likelihood of hypothesized trees given observed stratigraphic data. Likelihoods then are combined to evaluate trees. The resulting likelihood tree is nearly 30 steps longer (378.4 versus 350.5), but is considered more likely (given a 350.5-step matrix) than a tree of 350.5 steps. Both trees suggest that budding cladogenesis (where ancestors co-exist with descendants) was the most common pattern of speciation, although the likelihood tree is more emphatic on this point. Both suggest a trend towards increasing numbers of ornate species; however, whereas parsimony suggests the differential diversification of an ornate clade, likelihood suggests a strong tendency for inornate ancestors to have ornate descendants. A genus-level taxonomic revision is provided that is consistent with both trees and that attempts to reflect historical diversity patterns.

Key words: phylogeny, likelihood, fossils, Paleozoic, gastropods

Gastropods have a rich fossil record coupled with extensive ecologic and morphologic diversity among extant species. These factors make the clade an excellent model for testing macroevolutionary hypotheses (Bieler, 1992). Most macroevolutionary hypotheses make predictions about phylogenetic patterns. Therefore, robust phylogenetic estimates offer means of testing alternative macroevolutionary hypotheses. Examples of such hypotheses that have been tested in a phylogenetic context with fossil gastropod data include hypotheses about speciation patterns (Wagner and Erwin, 1995), predator-prey escalation (Carlson and Vermeij, 1996), phylogenetic constraints (Wagner, 1995a), and long-term trends (Wagner, 1996).

Unfortunately, fossilized character data for gastropods are limited almost entirely to shell characters, which likely are highly homoplastic (*e. g.* Harasewych, 1984; Kool, 1993). Phylogenetic methods such as parsimony likely will perform poorly with shell data because much

character congruence will reflect convergence rather than shared ancestry (Felsenstein, 1984; Archie, 1996). The dense fossil record of gastropods offers a potential antidote to the homoplasy problem because phylogenetic hypotheses make necessary predictions about durations, which in turn make probabilistic predictions about stratigraphic ranges. Accordingly, several workers have used stratigraphic data to test whether characters linking taxa are better explained as convergences than as homologies (*e. g.* Fisher, 1991, 1994; Huelsenbeck, 1994; Cheetham and Jackson, 1995; Wagner, 1995b).

This paper will attempt to address whether shell character data retain phylogenetic signal and whether incorporating stratigraphic data improves estimates of phylogenies. Shell character and stratigraphic data for Ordovician and Silurian members of the Lophospiroidea (= Lophospiridae + Trochonematidae) are analyzed using compatibility, parsimony, and maximum likelihood techniques to contrast alternative hypotheses about lophospiroid relationships and character evolution. The implications of the different results for macroevolutionary hypotheses and lophospiroid classification also are discussed.

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DATA AND ANALYSES

SHELL CHARACTER DATA, ANALYZED SPECIES, AND PARSIMONY

A previous phylogenetic analysis of lophospiroids used 57 characters and 150 character states to estimate relationships among 55 Ordovician species (Wagner, 1995b). The analysis presented here uses 95 characters encompassing 257 character states for 82 Ordovician and Silurian species. The increased number of character states reflects in part the addition of Silurian species with characters and character states unobserved among Ordovician species. Also, the characters were re-coded following Wagner [in press (a)]. Many characters from the 1995 analysis are divided into two or more characters that better reflect variations observed among Early Paleozoic gastropods. Nevertheless, 95 characters might appear to be a large number for a group of gastropods that previously were divided into only two families. However, a survey of numerous phylogenetic studies of gastropods shows that the ratio of shell characters to analyzed taxa increases as the taxonomic level of the analysis becomes finer [Wagner, in press (a)]. Also, lophospiroids are a morphologically diverse clade. Many more characters are needed to describe this diversity than are needed to describe any one species.

The characters are listed and described in Appendix 1. The character matrix is given in Appendix 2. Continuous characters are divided into ordered series using segment coding and then de-weighted so that the maximum difference equaled one step (Chappill, 1989). As a result, alternative trees often have fractional lengths. Other multi-state characters are treated as ordered if they represented a logical geometric series; otherwise, they are considered unordered. Some characters, such as the shapes and dimensions of the right and left ramps, vary both in symmetry (*i. e.* left and right being nearly identical) and dimensions. For such characters, symmetry versus asymmetry is coded as one character. Left and right characters are coded separately if they varied independently among asymmetric species. However, left and right characters necessarily covary on symmetric species, which leads to a conundrum: devising a coding scheme where the difference in left and right ramp shape accounts for one difference between two symmetrical species, two differences between two asymmetrical species, and two or three differences between a symmetrical and an asymmetrical species (one difference reflecting symmetry:asymmetry, with the third difference apparent only if both the left and right ramps differ). Step matrices (Swofford and Olsen, 1990) offer a potential solution, but these result in exorbitant run times. Instead, asymmetrical characters are weighted one-half of presence/absence characters, making changes among asymmetrical species equal to one step. Trees are rescaled using

a separate program that insures no "chimera" reconstructions (*e. g.* hypothesized symmetrical ancestors with different left and right sides), with the tree lengths now scaled as they would be by a step matrix.

Broader phylogenetic analyses [Wagner, in press (a)] suggest that lophospiroids are nested within the Murchisoniina, with species assigned to the genus *Ectomaria* representing the immediate outgroup. Therefore, *Ectomaria adelina*, which is both the earliest known *Ectomaria* and contemporaneous with the oldest lophospiroids, is included as an outgroup. Another contemporaneous murchisoniinae species, *Hormotoma simulatrix*, also is included as an outgroup.

Heuristic parsimony analyses using PAUP 4.0* (Swofford, 1998) found 36 trees of 350.8 steps. The illustrated tree (Fig. 1) is the parsimony tree with the fewest stratigraphic gaps, which satisfies the secondary role for stratigraphy advocated by Smith (1994). [This is equivalent to Clyde and Fisher's (1997) "Analysis 2."] The tree is discussed in greater detail below, but it is presented here to introduce the potential errors for the following sections. The 50 random addition replicates found an additional six islands of trees (Maddison, 1991) with minimum length trees of 380.5 or fewer steps. The phylogenetic reconstruction (Fig. 1) accounts for both stratigraphic ranges and character distributions. Both are important because species identical to reconstructed ancestral morphologies obviate the need for hypothesized range extensions (Fisher, 1991; Smith, 1994).

DO SHELL CHARACTERS CONTAIN PHYLOGENETIC SIGNAL?

Bandel and Geldmacher (1996) criticized a previous phylogenetic analysis of Ordovician lophospiroids by Wagner (1995b) because the resultant phylogenetic estimate linked *Trochonema* and allies to lophospiroids. Bandel and Geldmacher (1996) considered these to be distant relatives based on Triassic specimens. Those authors attributed Wagner's (1995b) results to pervasive homoplasy among shell characters. There is some support for Bandel and Geldmacher's (1996; hereafter B&G) hypothesis. Parsimony reconstructions based on soft anatomy suggest high frequencies of homoplasy among shell characters (*e. g.* Carlson and Vermeij, 1996; Haas, 1997). The utility of shell characters (on which this analysis necessarily relies) must be questioned and the B&G hypothesis must be tested before proceeding with further analyses.

Hypothesized phylogenies predict hierarchical structure among homologies. Conversely, a hypothesis of pervasive homoplasy (such as the B&G hypothesis) predicts little hierarchical signal among the characters. However, the B&G hypothesis does not predict an absence of congruence. Although the terms often are confounded

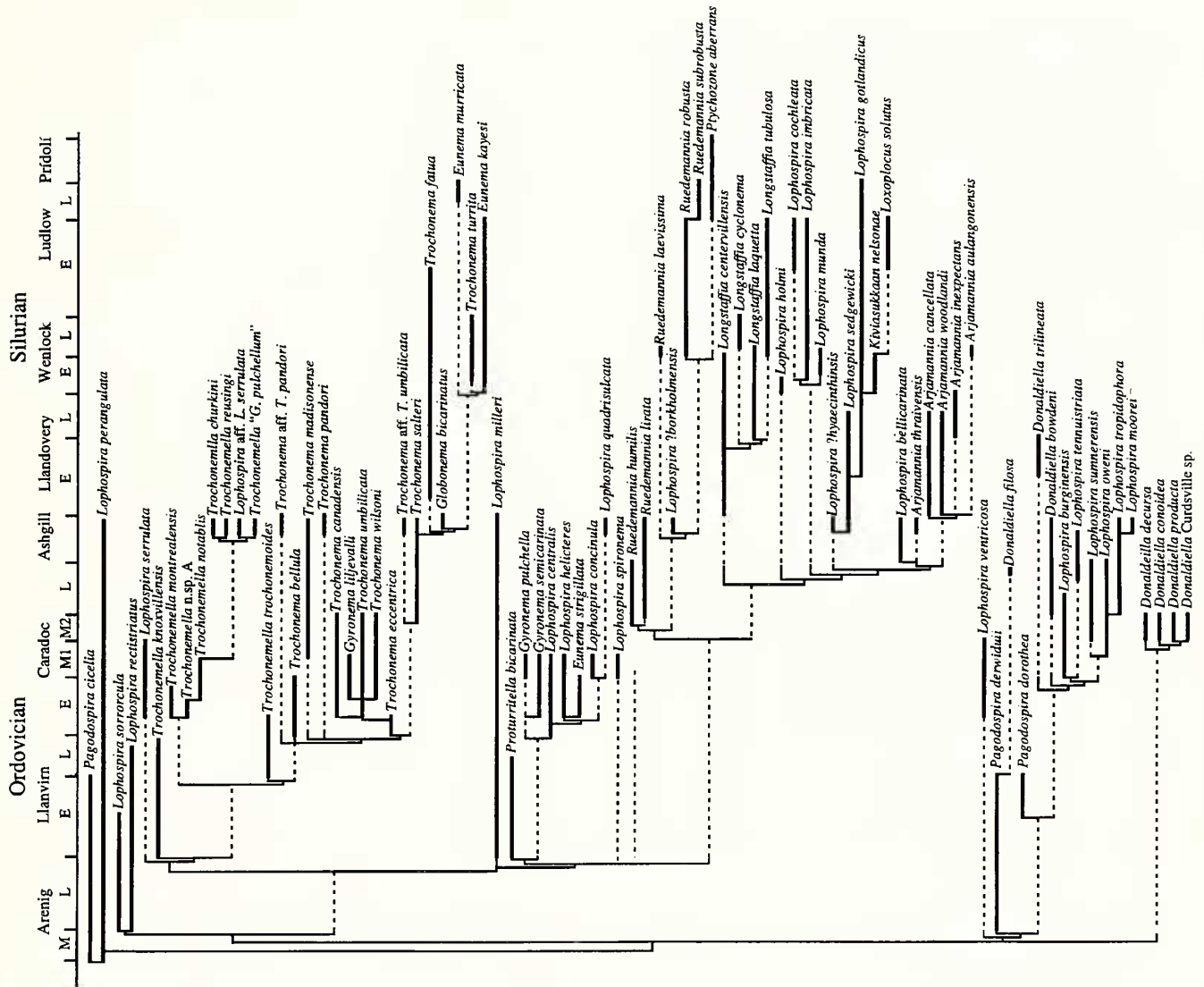


Fig. 1. Phylogenetic interpretation of one of 36 parsimony cladograms. This tree implies less stratigraphic debt than does any of the other 35 trees. Thin solid lines show estimated phylogenetic connections. Dashed lines show hypothesized unsampled lineages and taxa that are implicit to the phylogenetic hypothesis (*i. e.* range extensions *sensu* Smith, 1988, 1994; = ghost lineages and taxa *sensu* Norell, 1993). The tree posits 350.5 steps [consistency index (CI) = 0.316; retention index (RI) = 0.807] and 102 units of stratigraphic debt, with debt units based on the substages marked on the time scale. Species identical to hypothesized ancestors are linked directly to nodes and are considered ancestral to their apomorphic sister taxa here. [*Trochonemella* "G. pulchellum" is identical to *Trochonemella* BMNH 36364 in Appendix 2.]

(*e. g.* Bryant, 1992; Carpenter, 1992), hierarchy and congruence are not synonyms: congruence exists in non-hierarchical matrices (Källersjö *et al.*, 1992; Alroy, 1994) and even in randomly generated matrices (Archie, 1989; Faith and Cranston, 1991). However, whereas hypotheses of phylogeny and homology predict hierarchical congruence among characters, hypotheses of homoplasy predict non-hierarchical congruence. (The one exception to this expectation is when multicharacter complexes are homoplastic and patterned so that character combinations appear in the same order multiple times; however, this begins to violate another

important assumption of phylogenetic methods, *i. e.* the independence of characters.)

Several workers (*e. g.* Meacham, 1984, 1994; Sharkey, 1989, 1994; Alroy, 1994) have suggested using character compatibility (Le Quesne, 1969; Estabrook *et al.*, 1975) to evaluate hierarchical content of matrices. Two binary characters with pairings of (00), (10), (01), and (11) must have homoplasy in one or both characters. Such incompatible characters necessarily lack global hierarchy. Two binary characters with only three of the possible pairs [*e. g.* (00), (10), and (01) or (11)] are considered compatible

because they can be reconstructed on some trees without homoplasy. Characters with little homoplasy should form many compatible pairs whereas those with numerous homoplasies should form many incompatible pairs.

Alroy's (1994) Permutation Compatibility (PC) test is operationally similar to the Permutation Tail Probability test (Faith, 1991). PC tests whether the hierarchical structure of a character matrix is significantly greater than that of a randomly produced matrix. Alroy (1994) divided compatibility into two types: hierarchical [= "direct" of Sharkey (1994)] and general ("indirect"). The former describes pairs where combinations show a hierarchical arrangement [e. g. (00), (01), and (11)]. The latter describes pairs where there is neither necessary homoplasy nor implied hierarchy [e. g. (00), (01), and (10)]. Because phylogenetic hypotheses explicitly predict hierarchy, I used the PC test with 1,000 randomized matrices to determine if randomly permuted matrices ever retained the same level of hierarchical compatibility as did the real matrix. Lophospiroid character data yielded 1,389 hierarchically compatible pairs out of 8,930 possible pairs. (The test has been amended here to compare characters, not character states, as was done in Alroy's implementation). Permuted matrices typically showed approximately half as many pairs (Fig. 2). Thus, the matrix has more hierarchical structure than expected if congruence largely reflected random homoplasy, allowing us to reject the B&G hypothesis.

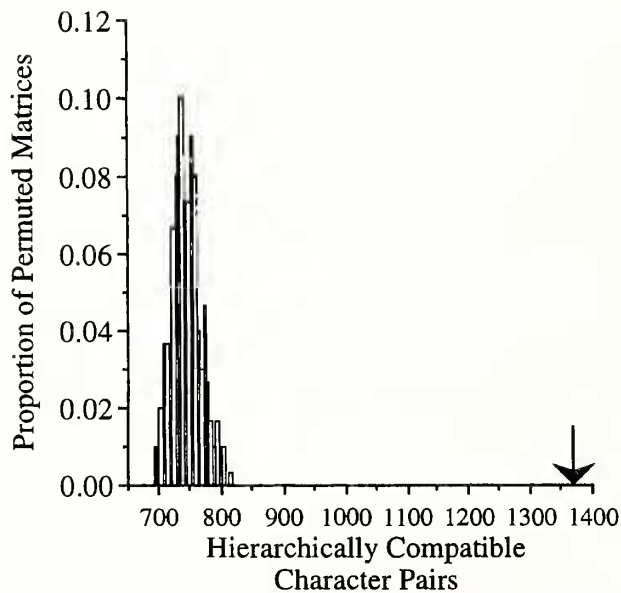


Fig. 2. Results of the Permutation Compatibility test (Alroy, 1994). The arrow denotes the observed value whereas the histogram gives the values generated by 1,000 random permutations of the character data. Hypothesized phylogeny predicts hierarchical compatibility whereas other hypotheses of character congruence (e. g. general convergence) do not. Thus, these results support (but do not demonstrate) the idea that there is phylogenetic signal among these characters.

DO WE NEED STRATIGRAPHIC DATA TO IMPROVE OUR ESTIMATES OF LOPHOSPIROID PHYLOGENY?

The presence of some hierarchical structure is no guarantee that there is not sufficient homoplasy to mislead parsimony. Simulation studies show that even low rates of randomly accrued homoplasy will result in inaccurate parsimony reconstructions of phylogeny (e. g. Mooers *et al.*, 1995). Finite numbers of character states (see Wagner, 1998c) insure that the probability of chance homoplasies confounding parsimony is not infinitesimal (Felsenstein, 1978). Patterned homoplasies (e. g. functional complexes) violate assumptions of character independence and also lead to inaccurate parsimony reconstructions (Lamboy, 1994; Archie, 1996). Finally, rates of character change that are not adequately reflected by character weighting (see Felsenstein, 1981) also yield inaccurate parsimony trees (Kuhner and Felsenstein, 1994).

Neontologists can test phylogenetic hypotheses derived from one data set by examining different character sets (e. g. different types of molecules). The hypothesis that congruence from the original data set reflects phylogeny predicts very similar patterns of congruence in other data sets (assuming that changes in one character set do not affect changes in the other; Templeton, 1983). Unfortunately, only a single character set is available for extinct taxa such as lophospiroids. However, phylogenetic hypotheses also make necessary predictions about temporal durations of taxa (see, e. g. Smith, 1988). Predictions about durations make probabilistic predictions about stratigraphic ranges (Paul, 1982; Strauss and Sadler, 1989). If a hypothesis makes predictions (necessary or probabilistic) about a data set, then those data offer a test of the hypothesis.

Additional factors suggest that stratigraphic data might improve estimates of lophospiroid phylogeny. Simulation studies [Wagner, in press (b)] show that phylogenetic error exaggerates the phylogenetically implied range extensions (Smith, 1988, 1994; "ghost" lineages and taxa *sensu* Norell, 1993) far more often than error underestimates range extensions. The exaggeration becomes worse as frequencies of change per character per branch increase, but it is pronounced at the frequencies of change posited by the parsimony tree for lophospiroids (i. e. $f = 0.042$ per character per branch). Thus, the long gaps in sampling posited in Fig. 1 are evidence that synapomorphies (*sensu* Sober, 1988) are homoplastic rather than homologous. For lophospiroids, most gaps are highly improbable given observed sampling distributions (Wagner, 1995b).

Another concern is that the hierarchical signal of the character matrix might decrease as geologically younger taxa are added. Suppose that geologically older species have morphotypes (00), (01), and (01), but that later species introduce morphotype (10). The characters no longer are

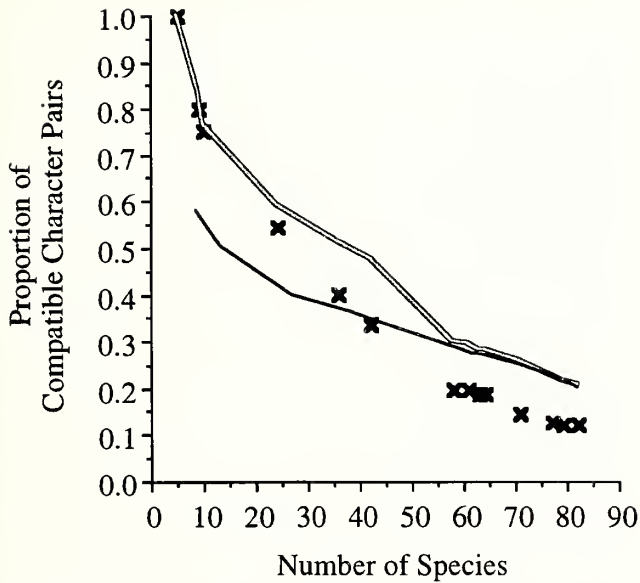


Fig. 3. Effects of geologically younger taxa on overall compatibility. As taxa are added over time, compatibility decreases. The white line gives the compatibility among all characters after X species are added to the matrix. Crosses give the compatibility among only the 73 characters informative for "early" (*i. e.* pre-Caradoc) relations. Thin black line gives the compatibilities for all characters when stratigraphic ranges are assigned at random.

compatible, and the younger species necessarily imply reversal or convergence. Conversely, suppose that the older species had states (00) and (11) and some geologically-younger species had (10). This suggests that the "younger" species is descended from a phylogenetic intermediate that was not sampled initially. The former scenario predicts decreased character compatibility whereas the latter does not.

I examined the effect of geologically younger taxa on character compatibility among lophospiroids using all character and also only the 73 characters that vary among early lophospiroid species (Fig. 3). (Late-appearing characters are not relevant to relationships among the oldest taxa.) Compatibility decreases markedly over time. Sampling so poor that species were effectively sampled at random through time relative to their phylogenetic position (as implied by abundant ghost lineages) predicts a very different pattern. One thousand randomizations of stratigraphic ranges show that compatibility should begin lower than observed and that the decrease over time should be much less precipitous (Fig. 3). The observed patterns are consistent with the idea that Late Ordovician and Silurian lophospiroids exhibited homoplasy among the characters that distinguish Early-Middle Ordovician lophospiroids.

A final concern is whether methods incorporating stratigraphic data perform better than does parsimony. ("Parsimony" here and throughout this paper denotes minimum steps evolution [Edwards and Cavalli-Sforza, 1964;

Kluge and Farris, 1969]; other methods using parsimony criteria [*e. g.* stratocladistics] are labeled differently.) To test this, I simulated morphologic evolution using the number of characters and states per character apparently available to lophospiroids. Character evolution was ordered or unordered reflecting the assumptions of the phylogenetic analysis (Appendix 1). In one round of analyses, log-probabilities of character change were proportional to the relative weighting of characters (*i. e.* "equiprobable change"; see Felsenstein, 1981). In a second round, rates of change varied among characters at random (*i. e.* "variable change"). Two different speciation models were used, one in which ancestral morphotypes survived cladogenesis and could produce any number of descendants ("budding cladogenesis") and one in which ancestral morphotypes became pseudo-extinct while giving rise to two distinct descendants ("bifurcating cladogenesis"). Sampling parameters derived from lophospiroid data (see Appendix 3) were used to sample six species. (A six-species limit was imposed so that exhaustive searches could be used.) Parsimony analyses then were run using the simulated character matrices. Matrices were maintained only if parsimony estimated the same steps per sampled taxon as the real lophospiroid tree (*i. e.* 350.5 steps per 82 taxa ? 25.5 steps per six taxa; hereafter: a 25.5-step matrix).

The simulations then had character matrices and fossil records that were similar to those observed for lophospiroids. The stratigraphic data then were used for three additional phylogenetic analyses: reweighting with the Stratigraphic Consistency Index (SCI; Huelsenbeck, 1994), stratocladistics (Fisher, 1994), and sieving with 95% confidence intervals (CIS; Wagner, 1995b). The results of the phylogenetic analyses were contrasted using Robinson and Foulds' (1981) metric, which measures the proportion of nodes that agree on two trees. (If multiple optimal trees were found, then the mean error was used.)

All methods incorporating stratigraphic data outperformed parsimony when simulated character matrices and simulated sampling matched observed parameters for lophospiroids (Fig. 4). In the best case, stratocladistics correctly reconstructed over 50% of the cladograms. Parsimony, meanwhile, correctly reconstructed under 15% of the cladograms. Stratigraphic methods are less successful when rates of character evolution are not proportional to character weighting, something that is true of parsimony and other phylogenetic methods (Kuhner and Felsenstein, 1994). However, stratigraphic methods are slightly less affected by such variation than is parsimony.

In summary, lophospiroid character data show too much compatibility to be dismissed as noise. However, reasons to question the parsimony estimate of phylogeny include: (1) many implied but statistically improbable sampling gaps, (2) decreasing hierarchical signal over time, and

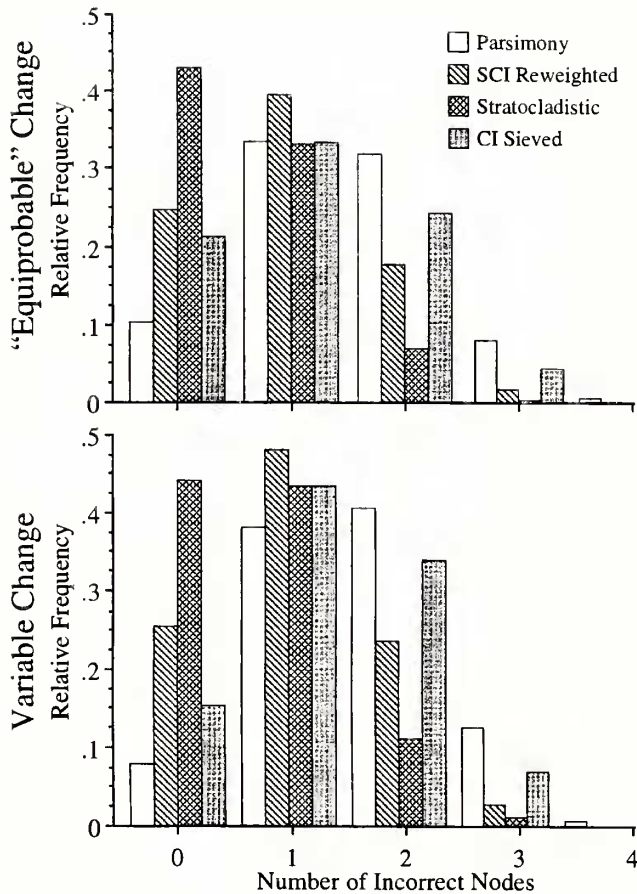


Fig. 4. Success of four phylogenetic methods for six-taxon simulations. The numbers reflect the number of incorrect nodes ("0" indicates a correct tree). The simulations use 95 characters and the same number of possible character states and character state orderings per character as lophospiroid data. Sampling intensities mimic observed sampling. "Equiprobable" evolution used probabilities of character change proportional to the character weight, whereas "variable" evolution used randomly assigned probabilities of change. Results are from budding cladogenesis, in which ancestral species can survive to yield any number of descendants, but the simulations produce nearly identical results when using bifurcating cladogenesis. Note that all three methods using stratigraphic data outperform parsimony. See text for additional discussion.

(3) superior performance of methods incorporating stratigraphic data in simulations.

WHY MAXIMUM LIKELIHOOD APPROACHES ARE USEFUL

How best to incorporate stratigraphic data into phylogenetic analyses is a non-trivial issue. I reject the position that stratigraphic data cannot improve phylogenetic estimates because such data are not hierarchically distributed (*e. g.* Eldredge and Cracraft, 1980; Rieppel and Grande, 1994; Smith, 1994). This only means that stratigraphic data do not offer inductive statements about phy-

logeny. If the goal is to test the predictions of phylogenetic statements, then one criterion applies: do estimated phylogenies make predictions about stratigraphic data? The syllogism is straightforward: if an inferred phylogeny is accurate, then taxa originated by particular times; if taxa originated by a particular time, then there is some probability that the known fossil record would be observed. Of course, the "deduction" is necessarily fuzzy, as stratigraphic data cannot demonstrate that a lineage had originated by any point in time, only that it is highly unlikely to have done so given observed data.

Unfortunately, the methods incorporating stratigraphic data used above all are unsatisfactory. Reweighting trees with SCI suffers because the SCI is greatest on pectinate trees (Siddall, 1996). Sieving trees with confidence intervals is not obviously predisposed toward favoring particular topologies. However, CIS suffers from focusing on particular nodes rather than the whole tree (Wagner, 1998b). Multiple independent tests and a traditional significance value of 0.05 should yield Type I errors (*i. e.* incorrectly rejecting the null) one time in every 20 tests. More damning, multiple tests should yield Type II errors (*i. e.* incorrectly accepting the null) even more frequently. For example, if there are ten gaps that are significant at a *p*-value of 0.10 each, then the CIS method will accept all of them. However, we expect only one of those gaps to be real.

An alternative approach with sounder logical justifications is to use likelihood to evaluate hypothesized trees. Stratocladistics actually represents a simple likelihood test. Summing steps is equivalent to summing negative logs of character change probabilities (Felsenstein, 1981) if: (1) probabilities for each character are the same among all clade members, (2) characters never change twice on the same branch, and (3) characters always evolve independently. The most likely tree then is the one invoking the fewest steps. Summing the negative log-probabilities of implied gaps (*i. e.* stratigraphic debt *sensu* Fisher, 1991, 1994) estimates the log-probability of a tree. Again, the most likely tree is the one implying the fewest stratigraphic gaps. The log-likelihood of the entire tree now equals the sum of stratigraphic debt and morphologic steps *if* the stratigraphic debt is weighted as:

$$-\ln(1 - R) = W * -\ln(P [c])$$

where $1 - R$ is the probability of not sampling a taxon over a particular interval (Foote and Raup, 1996), W is the weight of stratigraphic debt relative to characters, and $P [c]$ is the probability of character change along a branch.

Stratocladistics will retain nodes implying improbable gaps if they are supported by numerous synapomorphies. This offers a control for Type I errors which is lacking in the confidence interval method. Clyde and Fisher (1997) further justified stratocladistics on the grounds that

it uses the same optimality criterion to evaluate all of the data, which is the justification of "total evidence" analyses (e. g. Kluge and Wolf, 1993). However, stratocladistics requires *a priori* assumptions about sampling intensity (R) and frequencies of character change. As unknowns, both should be tested rather than assumed. Fortunately, the stratigraphic debt for any one tree implies an R , the likelihood of which can be assessed analytically (Foote, 1997). R 's predicting some debt are more likely than R 's predicting no debt (Wagner, 1998a), which means that statistically optimal trees can be "suboptimal" by stratocladistic criteria.

Nevertheless, the basic format of stratocladistics serves as a useful logical template. Because stratigraphy and morphology are independent data sets, the overall likelihood of any hypothesized tree is the likelihood of the tree given the character data times the likelihood of the tree given the stratigraphic data (Edwards, 1992). This is the approach that

will be taken in this paper (see also Wagner, 1998a).

CALCULATING LIKELIHOOD OF A HYPOTHEZED TREE GIVEN THE CHARACTER DATA

Congruence is an observable datum of a character matrix that is summarized by the parsimony length. The trees of interest are treated as hypotheses to be tested here. The likelihood of a hypothesized tree length (HL) yielding a parsimony length (PL) is proportional to the probability of observing the datum (PL) given the hypothesis (true tree length) (Edwards, 1992). Thus:

$$L [HL | PL] \propto P [PL | HL]$$

$P [PL | HL]$ cannot be calculated analytically, but simulations can be used to determine the frequencies of PL's derived from trees of known lengths. The simulations illustrated in Fig. 4 were based on six-taxon trees with 25.5-step character matrices. (Again, six-taxon trees

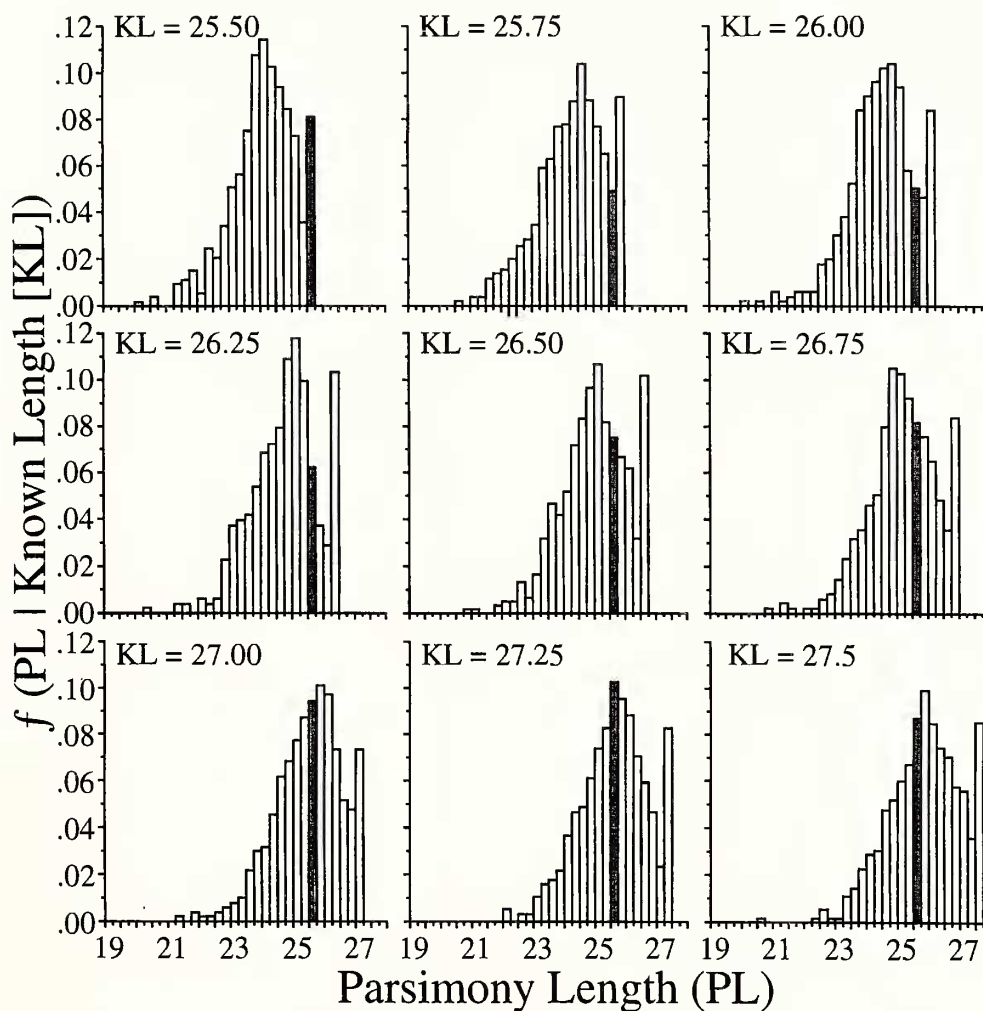


Fig. 5. The distributions of parsimony lengths given known lengths, based on simulations for six taxa with lophospiroid characters. The frequencies of matrices yielding parsimony lengths of 25.5 steps are highlighted. These match the number of steps per taxon as found for all 82 lophospiroids.

allowed use of exhaustive searches.) The frequencies of PL's given known lengths (*i. e. f* [PL | Known Length] in Fig. 5) indicate that a tree of 27 or 27.25 steps has a much higher probability of yielding a 25.5-step character matrix than does a tree of 25.5 steps. Thus:

$$L [\text{HL} = 27.25 \mid \text{PL} = 25.5] > L [\text{HL} = 25.5 \mid \text{PL} = 25.5]$$

This is best appreciated by examining the relative heights of the solid gray bars in Fig. 5, which approximate the likelihood of HL's given the observed congruence. The bar at 27.25 is the highest, indicating that this is the length most likely to have yielded the observed congruence.

One point not discussed above is that the simulations estimate $P[\text{PL} \mid \text{KL}]$ only if a particular hypothesis of character evolution is assumed. Fig. 5 illustrates the results when simulated character evolution is derived from the weighting scheme (see Felsenstein, 1981). Deviations from this models resulted in longer trees lengths becoming more likely and the shortest tree length becoming less likely (Wagner, 1998a). Thus, these results represent the highest possible likelihoods for parsimony hypotheses.

We need to evaluate 82-taxon phylogenies to evaluate lophospiroid phylogenies. This is accomplished by randomly selecting 13 six-taxon clades and one four-taxon clade (derived from a separate set of simulations not illustrated here). Parsimony lengths among random six-taxon clusters within lophospiroids varied from 15.8 to 29.6 steps. Therefore, true tree lengths were randomly selected from the range of true lengths that yielded parsimony lengths of 15.8 to 29.6 steps (*i. e.* 15.8 to 54.1 steps). Note that the use of a range of true lengths means that estimated probability does not assume clock-like rates of morphologic change (*contra* Norell and Novacek, 1997).

Parametric bootstrapping (see Huelsenbeck *et al.*, 1996) then assigned parsimony lengths to each true length. Assignments used distributions such as those illustrated in Fig. 5. The true lengths and parsimony lengths of the 14 subclades are then summed, which yields the likelihood distribution for hypothesized tree lengths given 82 taxa and lophospiroid character data (Fig. 6). Log-likelihoods are illustrated because the likelihoods of shorter trees are too low to be visible on a histogram.

Parametric bootstrapping never reconstructed any trees with both true and parsimony lengths of 350.5 steps. (This is not surprising, as the probability of doing so is approximately 10^{-14} , which requires several orders of magnitudes more replications than performed.) Because the likelihoods of tree lengths under 356 steps could not be estimated from parametric bootstrapping, I assigned log-likelihoods of that length (-10.415) to all shorter lengths.

Alroy (pers. comm., 1998) suggested that the likelihood estimates for the parsimony length might be too low because heuristic searches were used to estimate the initial parsimony length of 350.5 steps. However, for a hypothe-

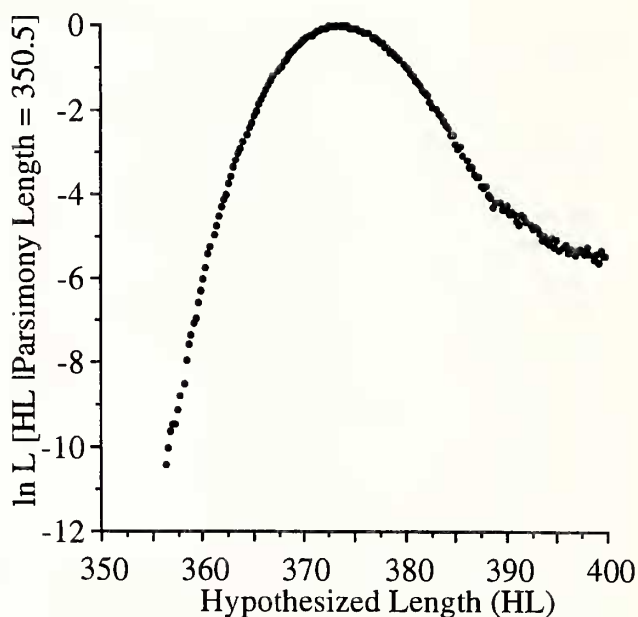


Fig. 6. Log-likelihoods of hypothesized tree lengths given a 350.5 step matrix for 82 taxa with lophospiroid characters. Note that trees 20-30 steps longer than the parsimony length are orders of magnitude more likely than are trees of 350.5 steps.

sized length of 350.5 to be as likely as a tree length of 370, the actual parsimony length must be around 330 steps. It seems improbable that heuristic searches could have missed by that much. Other aspects of the test *overestimate* the likelihoods of parsimony lengths (Wagner, 1998a). The test does not allow parsimony to confound homoplasy among subclades. Also, it uses the best-case model of character evolution (see above). All other models result in a lower probability of parsimony lengths equaling hypothesized lengths. These factors, coupled with the deliberate overestimate of parsimony length likelihood described above, mean that the tests used herein are quite conservative if one wishes to treat the parsimony tree as a null hypothesis.

CALCULATING LIKELIHOOD OF A HYPOTHE- SIZED TREE GIVEN STRATIGRAPHIC DATA

Continuous Stratigraphic Data

Wagner (1995b) used continuous stratigraphic data to estimate confidence intervals for lophospiroids. Huelsenbeck and Rannala's (1997) maximum likelihood test was applied using these data (see Appendix 3). As in the 1995 analysis, the "time" scale used here is actually the number of sampled units ("horizons") per stratigraphic interval. Thus, gaps through poorly sampled intervals are more likely than are gaps through well-sampled intervals, even if both intervals are of the same duration.

Huelsenbeck and Rannala's (1997) test is modified slightly here. The most important modification is that the

phylogeny is no longer considered a predictor of species' extinctions. This would be true if species evolved anagenetically. However, budding cladogenesis patterns predict only the latest possible origins of species. The parsimony tree (Fig. 1) illustrates possible examples of budding cladogenesis, as parsimony finds several plesiomorphic species known after their apomorphic sister taxa appear. ("Plesiomorphic species" are those that match inferred ancestral morphotypes.) Previous phylogenetic analyses suggest that budding cladogenesis was the predominant speciation pattern among lophospiroids (Wagner and Erwin, 1995). The exact probability of data given a hypothesized origination now is:

$$P[\text{FKA}, \text{LKA}, \text{H} \mid \text{HFA}, f] = f \left(\frac{(\text{LKA} - \text{FKA})^{\text{H}-2} f^{\text{H}} e^{-f}}{(\text{LKA} - \text{HFA}) \cdot (\text{H} - 2)!} \right) \quad \text{when } \text{H} \geq 2$$

$$= f e^{-f (\text{LKA} - \text{HFA})} \quad \text{when } \text{H} = 1$$

where FKA is the first-known appearance, LKA is the last-known appearance, HFA is the hypothesized first appearance, H is the number of horizons from which the species is known, and f is the proportion of horizons within a species range from which it is sampled (amended from Huelsenbeck and Rannala, 1997: equations 2 and 4).

The likelihood of a hypothesized origination time implicit to the inferred phylogeny now is:

$$L[\text{HFA}, \lambda \mid \text{FKA}, \text{LKA}, \text{H}] = c * \text{IPR}(I=1, I = \text{nodes} + \text{OTUs} - 1, P(\text{FKA}, \text{LKA}, \text{H} \mid \text{HFA}, \lambda))$$

(amended from Huelsenbeck and Rannala, 1997: equation 5) where c is an arbitrary constant that rescales each likelihood (L), so that the maximum likelihood is 1.0 (Edwards, 1992).

Discrete Stratigraphic Data

The stratigraphic debt implicit to an inferred phy-

logeny implies a particular R (Wagner, 1998a), the likelihood of which can be evaluated (Foote, 1997). ("Sampling intensity" here denotes the average proportion of species per interval that are sampled; Foote and Raup, 1996). If a species invokes four units of stratigraphic debt, then the phylogeny implies that the species was sampled in its fifth unit after diverging from its closest sampled relative. The phylogeny therefore implies a sampling intensity of 0.2 (*i. e.* one find in five tries). For an entire phylogeny, 90 units of stratigraphic debt distributed among ten species suggests an average sampling intensity of 0.1. Because phylogenies infer latest necessary divergences (Smith, 1988), stratigraphic debt gives the minimum implied gaps. A simple analytic estimate therefore is biased toward overestimating R , especially on large phylogenies (Wagner, 1998a), so R is best estimated using simulations.

Stratigraphic debt was calculated using the substages marked in Fig. 1. For the parsimony tree, there are 102 units of stratigraphic debt. Stratigraphic debts of 102 for 82 species (two of which are present in the earliest substage) imply an $R = 0.33$. (Note that an analytic $R = f(80, 182) = 0.44$ is substantially greater.)

Taxon ranges reflect both R and durations (which reflects extinction intensity, μ) (Sepkoski, 1975; Foote and Raup, 1996). As sampling becomes worse, ranges will decrease regardless of actual durations. In the extreme case of nearly infinitesimal R , the few observed species will each be known from single localities and all species will have ranges of one unit. Such clearly is not the case for lophospiroids (Fig. 7A). The most likely hypothesis for observed lophospiroid ranges is $R = 0.68$ per substage (Fig. 7B, with $\mu = 0.52$ per substage). Given the R associated with given

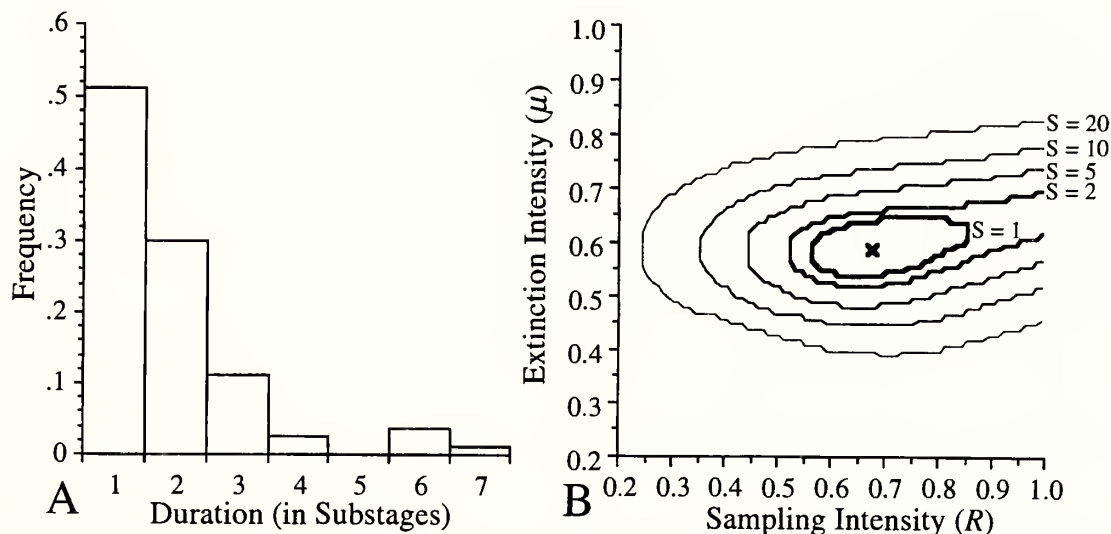


Fig. 7. Estimates of the likelihood of sampling intensities (R) and extinction intensities (μ). A. Distributions of observed ranges, with ranges measured by the major divisions shown in Fig. 1. B. Log-likelihoods for hypotheses that particular combinations of μ and R yielded the distribution shown in A. The maximum likelihood estimate is $R = 0.68$ per substage and $\mu = 0.52$ per substage.

amounts of stratigraphic debt, it now is possible to assess the likelihood of any given amount of stratigraphic debt (Fig. 8).

RESULTS

BASIC ASPECTS OF THE ALTERNATIVE TREES

Likelihoods were calculated using both methods for 100,000 trees from several different islands. Both methods found strongest support for the same tree (Fig. 9; hereafter, the ML tree). Traditional tree statistics are presented in Table 1 and the figure captions.

The ML tree is generally similar to the parsimony tree (Fig. 1) and also to the estimates provided in Wagner (1995a). *Trochonema* is again placed among *Trochonemella* spp., whereas other taxa previously assigned to the Trochonematidae (*e. g. Eunema, Gyronema, Protruritella*) are derived separately from traditional lophospirids. This corroborates previous several previous hypotheses (*e. g. Ulrich and Scofield, 1897; Wenz, 1938; Knight et al., 1960; Erwin, 1990*).

The ML tree (as the CIS tree before it) derives the problematic *Lophospira serrulata* directly from the contemporaneous *L. perangulata*. That species was previously linked by parsimony to the clade of *L. rectistriata*; here, parsimony links it to the *Trochonemella-Trochonema* clade. *L. serrulata* shares several homoplasies with other species regardless of where it is placed, including open coiling of the gerontic whorls, pronounced sutural and umbilical carinae, and sharp right and left ramp carinae. Notably, these features are shared with species known from the same sediments, such as *Trochonema umbilicata, Trochonemella*

Table 1. Properties and statistics of alternative phylogenetic hypotheses. (HG, hypothesized gaps in horizon-level sampling; HL, hypothesized tree length; L [H | r], likelihood of a hypothesis given the measurable data; ML, maximum likelihood; Pars, parsimony; PL, parsimony reconstruction of the character matrix; SD, hypothesized stratigraphic debt, with debt measured in the same stratigraphic units as "Ranges").

Tree	HL	L [HL PL]	SD	L [SD Ranges]	L [HG Horizons]
Pars	350.50	$<3 \times 10^{-5}$	102	5.95×10^{-6}	1.04×10^{-211}
ML	378.37	0.598	27	0.252	4.96×10^{-43}

notabilis, L. helicteres, and Eunema strigillata. These features are also homoplastic among these same taxa, which makes the assessment of these features as homoplastic on *L. serrulata* all the more plausible.

Multicharacter homoplasies suggest that characters did not evolve independently. However, the homoplastic characters appear in different orders among the different lineages (*i. e. morphotype 11* might be derived from 00 → 01 in some cases, 00 → 10 in others, and directly from 00 in still other cases). Also, the characters in question all vary freely in other parts of the clade. Finally, these characters sometimes present the only discernible differences among morphospecies. The initial assumptions of character independence almost certainly are violated, albeit "fuzzily." Sophisticated likelihood tests examining varying degrees of interdependence among characters offer one solution for this problem. However, it bears stressing that the likelihood method used here recovers a pattern that violates the initial assumptions whereas parsimony does not.

Regardless of the implications for character coding,

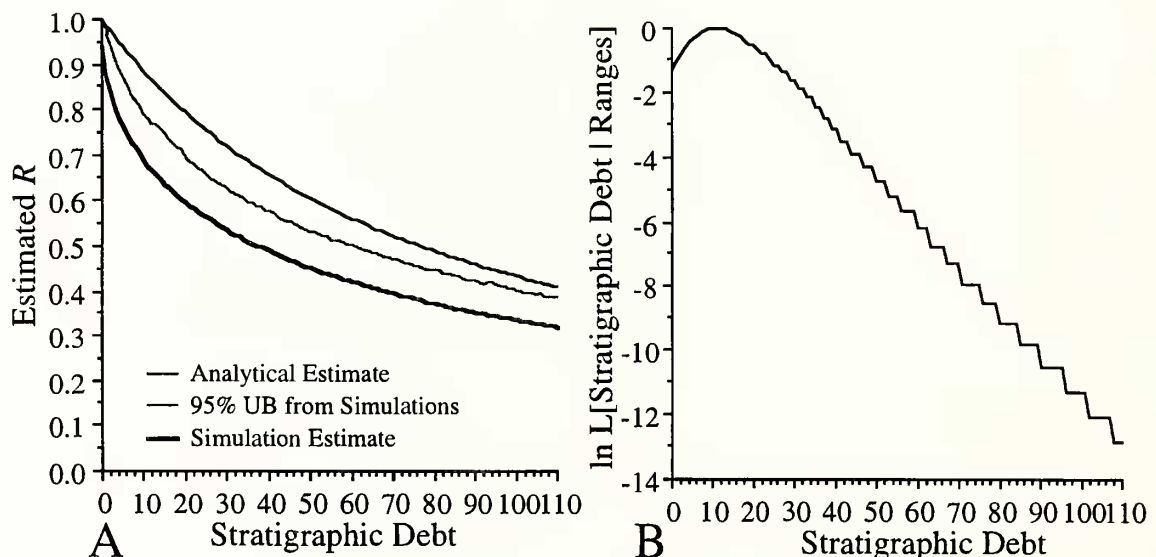


Fig. 8. A. Estimated sampling intensity (R) given stratigraphic debt distributed among 82 species (with two present in the first interval). Shown are the analytic solution, the average from 1,000 simulations and the 95%. B. Log-likelihoods of stratigraphic debts (see Fig. 7).

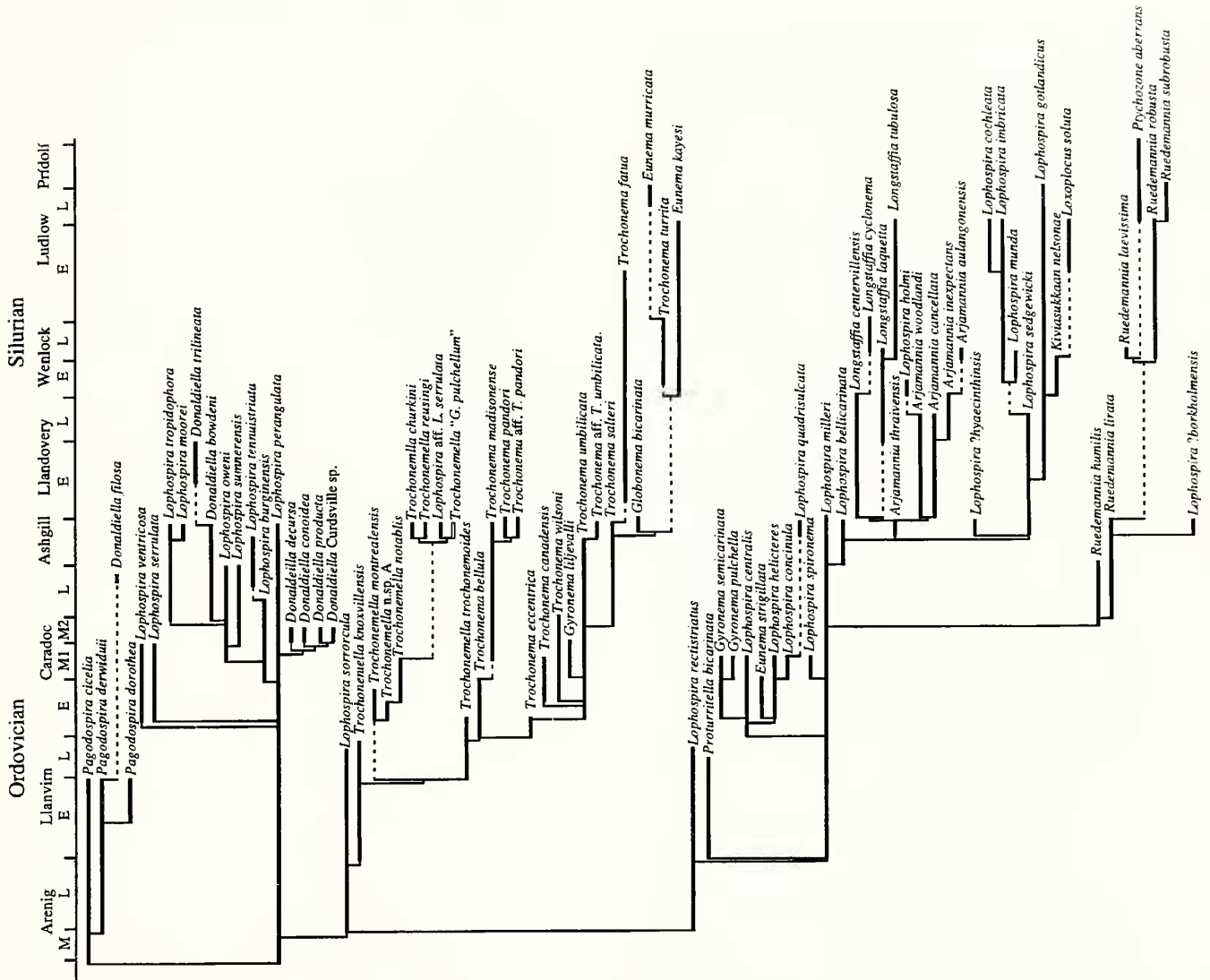


Fig. 9. Maximum likelihood estimate of lophospiroid phylogeny. The tree posits 378.4 steps (CI = 0.293; RI = 0.784) and 25 units of stratigraphic debt, with debt units based on the substages marked on the time scale. The tree is considered more likely not simply based on stratigraphic debt (Fig. 10) and continuous stratigraphic data (Table 1), but also on morphologic data (Fig. 8). As in Fig. 1, solid lines show estimated phylogenetic links and dashed lines denote ghost lineages or taxa.

the overall pattern is consistent with a hypothesis of strong functional or ecological convergence among these taxa. (Lophospiroids lacking these features are known from the same strata, so the characters cannot be dismissed simply as ecophenotypic variants.) Returning to the particular question of *Lophospira serrulata*, that species retains many plesiomorphic features. Small specimens are very similar to *L. perangulata*, save that the medial lira of the sinus keel is serrated and a prominent right ramp carina is present. (Note that "sinus keel" is used here instead of selenizone, as the latter term is used to denote a morphogenetic artifact of a slit. Sinus keels appear long before slits and the feature represents a separate homology that happens to be in

the same location as a slit.) If the additional synapomorphies realized on larger specimens are associated with a functional complex, then *L. serrulata* might be separated from *L. perangulata* by fewer evolutionary innovations than implied by the character coding.

Parsimony links *Donaldiella bowdeni* and other high-spined lophospiroids to trochiform species such as *Lophospira burginensis* which differs from the trees presented by Wagner (1995b). The ML tree differs by (1) placing only *D. bowdeni* and the Silurian *D. trilineata* in that clade, and (2) considering the characters associated with the high-spined morphology to be secondarily derived rather than primitive. All trees suggest that the earliest

lophospiroids were high-spined, corroborating Grabau's (1922) hypothesis about lophospiroid origins. However, the ML tree corroborates Ulrich and Scofield's (1897) hypothesis that *D. bowdeni* was derived from *L. oweni* rather than from older high-spined species.

LIKELIHOOD RATIO TESTS

Despite being nearly 10% longer than the most-parsimonious tree, the ML tree is orders of magnitude more likely than the parsimony tree given morphologic data alone (Table 1). (Again, the likelihood was calculated assuming that character evolution matched the weighting scheme of parsimony.) If variable rates of character change are used or if patterned homoplasies are included (both of which are biologically realistic), then shorter trees become even less likely whereas longer ones become more likely. The only model of evolution yields most likely lengths greater than 370 steps (*i. e.* the approximate most likely length gives a parsimony length of 350.5 steps among independently evolving lophospiroid characters): one in which there is no homoplasy. However, this hypothesis is falsified by the demonstration of incompatibility among lophospiroid characters. (In essence, this also falsifies the abductive predication of the parsimony proposition "if phylogenetic topology, then maximum congruence topology").

Likelihood ratio tests can be used to evaluate the relative support for competing hypotheses. The test statistic is:

$$\delta = 2 * (\ln L_1 - \ln L_0)$$

where L_0 is the likelihood of the null hypothesis (here, the parsimony tree) and L_1 is the likelihood of the test hypothesis (here, the likelihood tree) (Sokal and Rohlf, 1981: 695). The results of this test are given in Table 2. Ordinarily δ is evaluated using a chi-square distribution. Goldman (1993) cautioned against doing so when evaluating phylogenies and suggested using simulations to determine the distribution of δ instead. However, simulated δ -distributions differ from a chi-square distribution at low δ -values, but not at high ones (see Wagner, 1998a). The extremely high δ -values indicate that both morphologic and stratigraphic data provide significantly more support for the ML tree than they do for the parsimony tree.

Table 2. Log-likelihood ratio tests contrasting the parsimony estimate with the maximum likelihood estimate. " δ " gives the ratio test statistic and is evaluated using a Chi-square distribution.

Stratigraphic Likelihood	ln L [tree PL & Strat. Data]			p
	Parsimony	ML	δ	
Stratigraphic Debt	-22.45	-1.89	41.11	1.44×10^{-10}
Horizon Data	-496.22	-97.92	796.59	2.97×10^{-175}

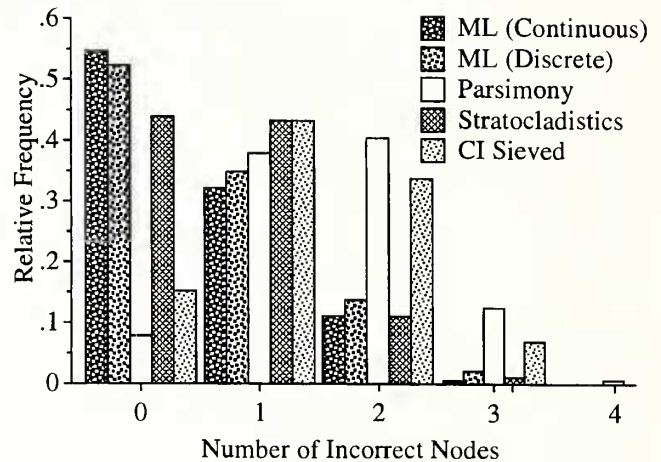


Fig. 10. Performance of maximum likelihood methods. "Continuous" uses the method of Huelsenbeck and Rannala (1997) to calculate stratigraphic likelihood; "Discrete" uses the method of Foote (1997) to calculate stratigraphic likelihood. The simulations used the "variable" model of character evolution, but the maximum likelihood estimates for morphologic change assumed an equiprobable model. Nevertheless, both methods outperformed parsimony, stratocladistics, and sieving with confidence intervals.

THE EFFICACY OF MAXIMUM LIKELIHOOD METHODS

An important consideration when contrasting different methods is relative performance under simple cases (Felsenstein, 1981, 1984). To this end, I conducted an additional set of simulations that contrasted the relative efficacy of the two maximum likelihood methods with that of parsimony, stratocladistics, and confidence interval sieving. Simulations were conducted using the variable rate model of character evolution described above (see Fig. 4). Note that the model of character change did not match the assumptions of the likelihood estimates of morphologic change. In addition, simulated sampling was made more variable, with sampling densities and sampling opportunities varying from interval to interval.

Both methods perform far better than does parsimony (Fig. 10), and both also outperform the SCI, CIS, and stratocladistics. Huelsenbeck and Rannala's (1997) method does somewhat better than does the debt-likelihood test. This is unsurprising because Huelsenbeck and Rannala's (1997) method can distinguish the relative importance of particular gaps whereas the former cannot. Interestingly, stratocladistics frequently derived the same trees for simulated clades as did maximum likelihood. The stratocladistic and CIS trees were both very similar to the maximum likelihood trees with lophospiroid data. The general congruence among these methods and the superiority of these methods over parsimony in simplified simulations both suggest that the ML estimate to be a better summary of lophospiroid evolution than is the parsimony tree.

DISCUSSION

EVOLUTIONARY IMPLICATIONS OF THE PHYLOGENETIC ESTIMATES

Accurate phylogenies are premises of many tests of macroevolutionary hypotheses (Harvey and Pagel, 1991). When presented with rival estimates of phylogeny, it is important to explore whether the topologic differences affect general macroevolutionary interpretations (Donoghue and Ackerly, 1996; Wagner, 1997).

SPECIATION PATTERNS

Initial phylogenetic estimates suggested that budding cladogenesis was the most common speciation pattern within lophospiroids (Wagner and Erwin, 1995). This study also found a positive association between species' durations and numbers of apparent descendant species. Few patterns were found consistent with either bifurcating cladogenesis or anagenesis, both of which explicitly predict that ancestral and derived species did not co-occur. (Note that a "species" here is a unique combination of character states.) Budding cladogenesis does not demonstrate any particular speciation process. However, it is consistent with processes such as peripheral isolation (Mayr, 1963), shifting-balances (Wright, 1931; but see Provine, 1986), and punctuated equilibrium (Gould, 1982) and inconsistent with processes such as selective divergence (Darwin, 1859) and vicariance (Brooks and McLennan, 1991).

Both the parsimony and ML trees corroborate the original conclusions about speciation patterns. There are 18 taxa with plesiomorphic sister species on the parsimony tree. In 15 of those cases, the plesiomorphic taxon co-occurs with the derived sister taxon. There are 49 species with plesiomorphic sister species on the ML tree, 36 of which co-occur with their putative ancestor. On both trees, significantly more cases are consistent with budding cladogenesis than with anagenesis or bifurcating cladogenesis (parsimony: $p = 1.32 \times 10^{-3}$; ML: $p = 1.42 \times 10^{-4}$, based on a standard binomial test assuming a 50:50 distribution). However, one major difference exists. The parsimony tree posits no species with multiple descendants whereas the ML tree posits several species with two or more descendants. Moreover, there is a strong association between duration and the apparent number of descendants on the ML tree (Kendall's $\tau = 0.391$; $p = 2.44 \times 10^{-7}$; Sokal and Rohlf, 1981: 429). Models predicting budding cladogenic patterns are generally consistent with the pattern shown by the ML tree. However, it is not clear that any speciation models predict the pattern shown by the parsimony tree, where species such as *Lophospira perangulata* produce a single daughter taxon early and then persist many millions of years with no additional daughter taxa.

TRENDS

Wagner (1996) documented active trends for several shell features among Ordovician-Silurian gastropods, including lophospiroids. One of these trends, the reduction of the sinus, is clearly observable among lophospiroids. Early species such as *Lophospira perangulata* have wide, deep sinuses that curve continuously back toward the sinus keel. Similar sinuses are retained among species classified as *Donaldiella* and in some *Lophospira* subclades (e. g. the *L. burginensis* clade). However, reduction of the sinus happens in parallel among derived *Trochonemella* (i. e. the clade including *T. montrealensis* and derived *Trochonema* (i. e. the clade including *T. umbilicata*). Note that the common ancestor of those two clades (i. e. species similar to *Trochonemella knoxvillensis* and *T. trochonemoides*), retained a *L. perangulata*-like sinus. A similar pattern of sinus reduction is observed among species in the clade including *L. milleri*). It should be noted that the trend as described at this level can be inferred from the parsimony and ML trees.

Additional parallelisms concerning the sinus exist on both estimated trees. In the case of derived *Trochonema* and the clade including *Lophospira centralis*, sinuses lose most of their curvature and retreat nearly straight to the sinus keel. A parallel reduction of the sinus keel is observed within both clades. Lophospiroids primitively possess a trilineate sinus keel, with a strong, sharp, medial lira bordered by two sharp and somewhat weaker peripheral lira. Broader analyses [Wagner, in press (a)] imply that the peripheral lirae of lophospiroids are homologous with the peripheral lira of other early Murchisoniinae (e. g. *Hormotoma* and *Eotomaria*) whereas the medial lira is a synapomorphy of early lophospiroids. The peripheral lirae are lost on *Trochonema* and twice lost within the *L. centralis* clade (i. e. *Eunema* and *Gyronema* spp.). The peripheral lirae also are lost in *Proturritella* and the *Kiviasukkaan-Loxoplocus* clade. Thus, the single peripheral keel of species previously assigned to the Trochonematoidea (e. g. Knight *et al.*, 1960) appears to be the medial lira of primitive lophospiroids. The reduction of the sinus keel precedes the reduction of the sinus among *Trochonema* spp., because species such as *T. bellula* and *T. pandori* possess only the medial lira but retain curved and fairly wide sinuses. Conversely, the reduction of the sinus precedes the reduction of the sinus keel among the *L. centralis* clade, because species such as *L. centralis* and *L. helicteres* possess shallow, straight sinuses but retain a trilineate sinus keel. Similar mosaic patterns of sinus and sinus-keel reduction are observed within other gastropod clades [Wagner, in press (a)]. Thus, the characters clearly are independent homologues in that a change in one does not necessitate an immediate change in the others.

However, the overall pattern suggests some sort of biological (*e. g.* functional) association.

Bandel and Geldmacher (1996) have stated that species such as *Trochonema* and *Eunema* could not be derived from ancestors with sinuses and/or slits and thus could not be lophospiroids. However, early *Trochonema* spp. possess a lophospiroid sinus that is reduced or entirely lost in derived species. *Eunema* spp. retain a derived sinus observed in species previously assigned to *Lophospira* (*e. g.* "*L.*" *centralis*). Sinus reduction obviously was common among Ordovician and Silurian lophospiroids. A slit is an uncommon feature among lophospiroids, but likely evolved at least three times within the clade. Derived *Trochonemella* spp. such as *T. notablis* are one such group of taxa, but primitive species such as *T. knoxvillensis* and *T. trochonemoides* clearly did not possess slits. Thus, whether

Trochonema or *Eunema* could have slit-bearing ancestors is irrelevant, as neither ML nor parsimony trees posit slit-bearing ancestors for either taxon.

Parsimony and ML trees suggest very different patterns of ornament evolution. The increasing number of ornate gastropod taxa over the Phanerozoic is a well-documented trend (*e. g.* Vermeij, 1977). Ornament is uncommon among lophospiroids until the Late Ordovician. Conversely, most Silurian lophospiroids had at least some ornament. The parsimony tree suggests that ornament arose four times and was subsequently lost four times (Fig. 11). (The reconstructions on the parsimony tree are unambiguous and thus not affected by optimization assumptions.) Parsimony also suggests that ornate taxa were substantially more diverse in the Middle Ordovician than sampling alone would imply. Hypothesized ornate range exten-

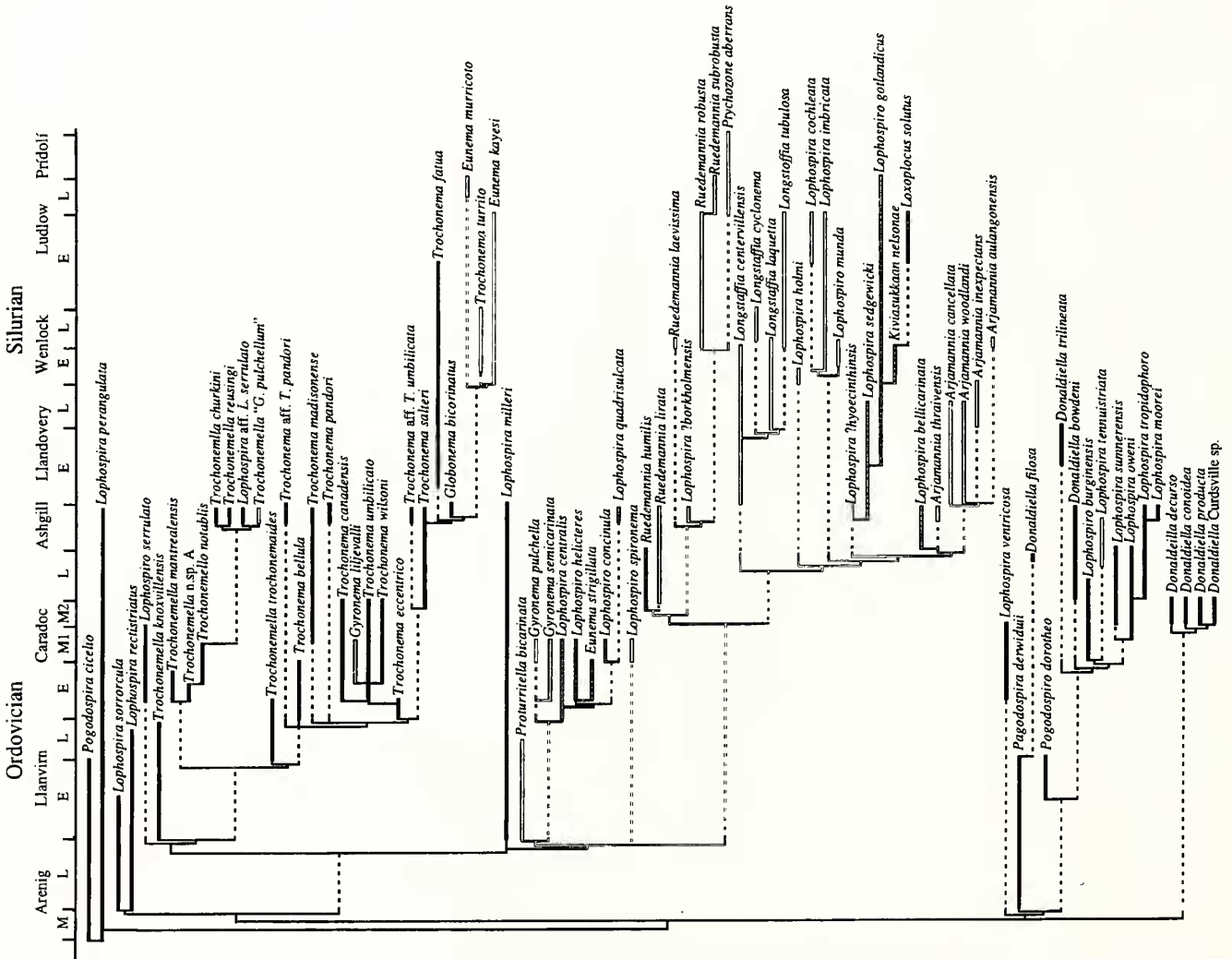


Fig. 11. Patterns of ornament evolution as posited by parsimony. Black branches denote primitively inornate species, gray branches denote secondarily inornate species, and white branches denote ornate species. Note that the tree posits a much earlier divergence of ornate species than observed in the fossil record, resulting in hypotheses of many ornate ghost taxa (*i. e.* white dashed lines).

1995). Simulations further suggest that parsimony is even less successful when transition patterns are biased (Kuhner and Felsenstein, 1994; Lamboy, 1994). Second, it is impossible to code ornament characters in a way that is neutral with regard to all possible patterns of evolution. Some species possess ornament throughout the shell, but species such as *Ruedemannia lirata* and *Arjamannia thraivensis* possess ornament only on the left ramp. In some non-lophospiroids, ornament occurs only on the right ramp. Thus, the presence and absence of ornament must be scored separately for both ramps. The result is that completely ornate species share two synapomorphies instead of one; if evolution goes from completely inornate to completely ornate (e. g. *Lophospira milleri* to *Proturritella bicarinata*), then parsimony counts two steps instead of one. A third and related reason is that similar characters were coded as synapomorphic (*sensu* Sober, 1988), if only at basic levels. For example, a species with coarse, broadly-spaced ornament on the left ramp shared the presence of left ramp ornament (character 87) with a species with fine, densely-packed ornament. Additional characters (e. g. characters 88 and 89) then were used to distinguish the two. This assumes that it is easier to modify a character than it is to evolve it, which many workers regard as the lesser assumption (e. g. Hennig, 1966).

The trend toward increasing numbers of ornate species highlights a potential strength of the maximum likelihood method over parsimony. Parsimony is ill-equipped to deal with biased transitions and character transitions that cannot be neatly coded. As such, the pattern of evolution shown in Fig. 12 predicts that parsimony results such as shown in Fig. 11 should be probable. However, the maximum likelihood analysis (with the help of stratigraphic data) was able to recover a pattern of evolution that was at odds with the initial assumptions.

The effect of initial assumptions about character change has additional implications. The ML tree suggests a trend towards increasing numbers of ornate species induced by a tendency for inornate ancestors to yield ornate descendants. The parsimony tree suggests a trend driven by a very speciose ornate clade. Several workers (e. g. Wright, 1967; Eldredge and Gould, 1972; Stanley, 1975; Vrba and Eldredge, 1984) hold that differential speciation might induce trends and that morphologic evolution might be random with respect to those trends (*i. e.* "Wright's Rule"; Gould, 1977). By minimizing the number of times characters arose and by maximizing the number of taxa linked by those characters, parsimony might be biased towards results consistent with "species selection" rather than with driven trends. Lophospiroids offer a possible example of this bias.

RECOMMENDED TAXONOMIC REVISIONS

Phylogenetic frameworks serve as a basis for taxo-

mic classification, which in turn can convey historical patterns of biodiversity to non-specialists. Conveying diversity patterns taxonomically is not simple. Some workers (e. g. Eldredge and Novacek, 1985; Smith and Patterson, 1988) argue that only monophyletic supraspecific taxa can reflect historical diversity patterns. If so, then phylogenetic systematics (Hennig, 1966) is appropriate. However, other workers use higher taxa as proxies for species in diversity studies because higher taxa are less prone to sampling biases than are species (e. g. Raup, 1979; Sepkoski, 1979, 1993; Raup and Boyajian, 1988). Paraphyletic and monophyletic taxa both are excellent proxies for extant species diversities (Williams and Gaston, 1994; Andersen, 1995; Balmford *et al.*, 1996). Both simulation (Sepkoski and Kendrick, 1993; Maley *et al.*, 1997) and empirical studies (Wagner, 1995c) indicate that taxonomic schemes including paraphyletic taxa portray species-level diversity patterns as well as or better than do those using monophyletic taxa alone. Including paraphyla becomes especially important when rates of cladogenesis and/or extinction or sampling intensities vary over time (Wagner, 1995c). Thus, a taxonomic scheme designed to reflect historical diversity patterns should include paraphyletic taxa lest it be biased against depicting particular patterns.

Evolutionary systematics (Simpson, 1961) allows for paraphyletic taxa, but evolutionary systematics has no explicit, repeatable criteria for delimiting such taxa (Hull, 1967; note that the same actually is true of Hennigian systematics; Tassy, 1988). Phylogenies are nothing more than artifacts of speciation and extinction rates (Sepkoski, 1987). Such an evolutionary parameter can be used to delimit "real" groups in a statistical sense. For example, quantitative analyses of net rates of cladogenesis in primates (Purvis *et al.*, 1995) and rates of morphologic change in rostroconch molluscs (Wagner, 1997) separate paraphyletic groups from monophyletic ones. Unfortunately, demonstrating that sets of species belong to statistically distinguishable groups requires large sample sizes, much larger than is available for defining genera or probably even families. Estabrook (1986) proposed integrating phenetic dissimilarity with phylogenetic topology to delimit higher taxa. This has the advantage of being fully repeatable once criteria are made explicit. However, if rates of morphologic evolution vary over time or across a clade, then more higher taxa will unite very different numbers of species and thus will not portray historical biodiversity accurately.

Although based on the ML tree, the generic definitions presented here would be nearly identical if derived from the parsimony tree. The lack of explicit criteria for delimiting genera does not interfere with a generic revision that better reflects historical diversity patterns than current generic schemes do (Fig. 13). For example, *Lophospira*

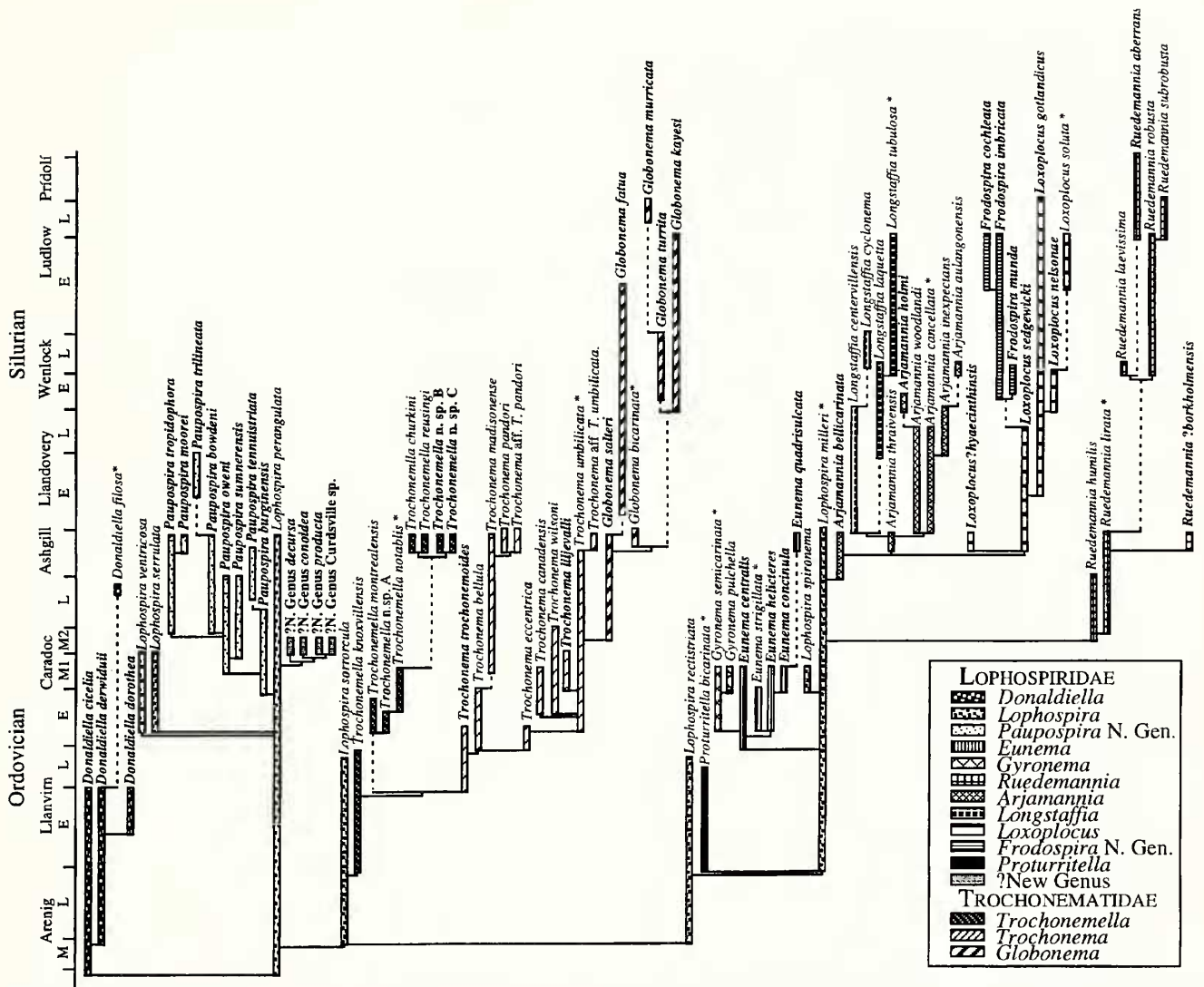


Fig. 13. Proposed taxonomic revisions. "*" denotes the type species of each genus. "Proturrutella" is retained because additional species not available for this analysis might belong there. Formal designation of "?New Genus" is withheld pending additional analyses, because it is possible that those species are instead affiliated with *Donaldiella filosa*, the type species of *Donaldiella*. If so, then the species here placed in *Donaldiella* should be returned to *Pagodospira*. See Appendix 4 for necessary rediagnoses and redefinitions.

bellicarinata could be assigned to either *Arjamannia* or *Loxoplocus*; in either case, one genus appears in the Late Caradoc whereas the other appears in the Ashgill. However, retaining all *Arjamannia* and *Loxoplocus* spp. in *Lophospira* results in a taxonomy that ignores the derivation of a diverse clade whose sister taxa (*i. e.* other derivatives of *L. milleri* such as *Ruedemannia* and the *Eunema*-*Gyronema* clade) are separated into one or more genera.

In some cases, the revisions simply update lophospiroid taxonomy. Many of the species analyzed here were originally classified before *Lophospira* was partitioned into additional genera. Initial diagnoses of new genera were not accompanied by exhaustive revisions of the entire clade,

resulting in a highly polyphyletic *Lophospira*. This is remedied to make *Lophospira* a paraphyletic group. Other cases involve redefining and rediagnosing obviously polyphyletic genera. For example, *Eunema* previously has been diagnosed by high translation (*sensu* Raup, 1966), the absence of a sinus and a medial keel. A sinus actually is present in the type species, albeit a shallow V-shaped one that is shared with some species formerly placed in *Lophospira* (all now reclassified as *Eunema*). In the redefinition presented here, only the type species lacks a trilincate sinus keel. However, the loss of a peripheral lira represents a derived condition that happened multiple times and therefore cannot unequivocally diagnose genera.

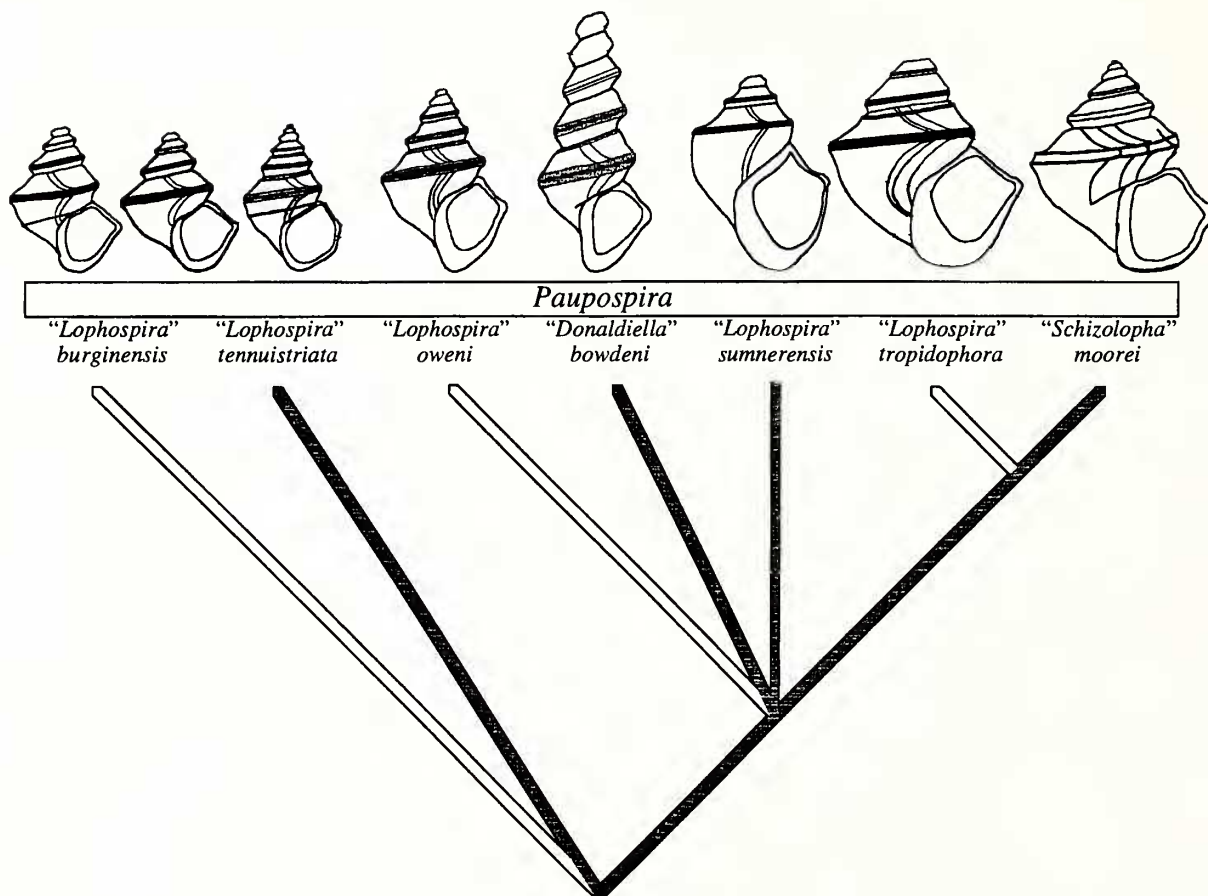


Fig. 14. Cladogram of *Paupospira* highlighting the important morphologic features of the clade. White branches denote zero-length branches (*i. e.* species identical to hypothesized ancestral morphotypes).

Patterson and Smith (1987) suggested that some diversity patterns inferred from taxic data might be artifacts of paraphyly. However, if a paraphyletic taxon's disappearance is not due to its sole species anagenetically transforming into a species placed in a different higher taxon, then its disappearance necessarily reflects the extinction of at least one species. Because paraphyletic taxa necessarily are older than their monophyletic "descendants," paraphyla often have higher standing diversities than their monophyletic "daughters" (Uhen, 1996) and thus require greater numbers of species extinctions to be terminated. For example, *Trochonemella* is paraphyletic relative to *Trochonema*, which in turn is paraphyletic relative to *Globonema*. However, the extinctions of *Trochonemella* and *Trochonema* in the Ashgill represents the loss of eight species (as well as the disappearance of particular morphotypes). *Globonema* represents two survivors, so the 2:1 casualties:survivors ratio implied by genera underestimates the 4:1 ratio implied by species. Alternative classifications fare worse. Any monophyletic definition including all members of the clade fails to register the extinction.

Conversely, reduced monophyletic definitions recognizing only the clades terminated in the Ashgill fail to recognize that the group diverged during the Middle Ordovician. A new monophyletic genus, *Paupospira*, also illustrates how strictly monophyletic higher taxa can obfuscate historical patterns. That genus is nearly eliminated by the end-Ordovician extinction, but a sole survivor is known from the Llandovery. The genus' demise somewhat misleadingly now represents a "background" extinction (Jablonski, 1986).

CONCLUSIONS

Although malacologists have questioned the utility of shell characters in phylogenetic analyses, shell character data for Ordovician-Silurian lophospiroids show compatibility similar to that expected if those data do retain hierarchical (phylogenetic) signal. Nevertheless, truly hierarchical signal among the clade as a whole and geologically older taxa in particular decreases with the addition of geologically younger taxa. Phylogenetic methods incorporat-

ing stratigraphic data outperform parsimony for simulated clades with similar fossil records and the same number of characters and character states as lophospiroids. Correspondingly, the parsimony estimate of lophospiroid phylogeny posits many more gaps than plausible given the quality of the lophospiroid record.

Likelihood tests support a tree that is 30 steps longer but nevertheless is more likely based on both morphologic and stratigraphic data. Both trees suggest that budding cladogenesis was the dominant speciation pattern, and both portray trends toward increasing numbers of ornate species. However, the likelihood tree depicts a strong association between duration and proclivity at the species level whereas the parsimony tree does not. Also, the likelihood tree suggests that the ornament trend was driven by the acquisition of ornament being far more common than its loss. Parsimony suggests that ornate clades were simply more diverse than were inornate clades. At least in this example, parsimony appears biased toward results suggesting patterns consistent with "species-selection." Lophospiroids highlight the utility of gastropods as a model group for testing macroevolutionary hypotheses. However, lophospiroids also highlight the importance of developing phylogenetic methods in whose results we can be more confident.

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APPENDIX 1

CHARACTERS AND CHARACTER STATES

Character state codings follow Wagner [in press (a)]. Lophospiroids do not possess all of the states available in some multistate characters developed for that analysis; therefore, in the following list, the plesiomorphic state for lophophorids is not coded "1" in all cases, and some character states appear to be missing. The character coding has not been adjusted herein, so that lophospiroids can be easily compared with other gastropods.

1. Sinus (broad cleft in shell, culminating at presumed location of anus): (1) absent; (2) present. Weight 1.
2. Sinus depth [as described by general angle of retreat by sinus; continuous character, ranging from almost 0° to 40°; really a shape metric, as true depth is a product of angle of retreat, sinus width (character 3), and curvature of retreat (character 4)]: (1) >0°; (2) ~10°; (3) ~20°; (4) ~30°; (5) ~40°. Ordered; weight 0.25.
3. Sinus width [as described by angle passing from center of aperture through top and bottom of sinus; continuous character, with states broken into just above/below sinus apex (1), halfway between top/bottom of ramp and sinus apex (2), coinciding with top/bottom of ramp (3), and beyond top/bottom of ramp (4)]; coding the position of the onset of the sinus relative to the top/bottom of the ramps rather than the absolute width accommodates the fact that changes in ramp lengths and orientations also will change sinus width as an artifact; this coding scheme focuses only on differences clearly attributable to the sinus itself]: (1) just above SK; (2) between SK and RR; (3) at RR. Ordered; weight 0.5.
4. Sinus shape [describing general trend of sinus; nearly straight up to sinus apex (*i. e.* V-shaped) or curving back continuously; this describes the shape of the curve whereas sinus depth (character 2) describes the general angle of retreat]: (2) straight; (3) continuous. Weight 0.5.
5. Crenulated aperture [in which apertural margin generates "zig-zag" growth lines]: (1) absent; (2) present. Weight 1.
6. Sigma-shaped aperture: (1) absent; (2) intersection between base and alveolae curved (yielding reverse sigma) instead of planar or angular. Weight 1.
7. Prominence of growth lines (GL) [evaluated only by comparison with both different specimens known from same preservational conditions and similar specimens from different preservational conditions]: (2) weak; (3) fine sharp; (4) strong. Ordered; weight 0.5.
8. Imbricated GLs [alternating growth lines appreciably stronger than others; considered present only if imbrications obviously are patterned, as random imbrications can occur due to shell repair or on gerontic whorls of some species; growth line prominence is coded based on weaker growth lines]: (1) absent; (2) weak; (3) moderate; (4) strong. Unordered; weight 1.
9. Sinus keel (SK) width [originally thought to be morphologic artifact of a slit or a "notch," however, appearing on slitless specimens and the seemingly mythical "notch" has never been documented; continuous character, where 360(equals circumference of aperture): (1) ~5°; (2) ~10°; (3) ~15°; (4) ~20°; (5) ~25°; (6) ~30°. Ordered; weight 0.2.
10. Peripheral lirae (PL) [two lirae on bilineate peripheral bands (or outer two on trilineate bands of lophospiroids); in some cases, might be produced by placing a slit within a medial lira (see below); however, not occurring on all species with slits and many species with peripheral lira clearly do not have slits]: (1) absent; (2) present. Weight 1.
11. PL type: (1) threads with round profile (*e. g.* *Ruedemannia*); (2) threads with sharp profile (*e. g.* *Ectomaria* or *Lophospira*). Weight 1.
12. PL strength: (2) weak (clearly visible but casting little relief); (3) moderate (casting noticeable relief); (4) strong (clearly projecting from shell). Ordered; weight 0.5.
13. Medial lira (ML) [= "notch keel" or "sinus keel"; present with peripheral lirae (character 10) only if there is ontogenetic change (character 25) or if peripheral band is trilineate; carina at the apex of the sinus]: (1) absent; (2) present. Weight 1.
14. ML type [as seen in profile]: (1) round, of equal "height" and width (*e. g.* *Ruedemannia*); (2) sharp, of equal "height" and width (*e. g.* *Lophospira*). Weight 1.
15. ML strength: (1) extremely weak (barely visible, casting almost no relief); (2) weak (clearly visible but casting little relief); (3) moderate (casting noticeable relief); (4) strong (clearly projecting from shell). Ordered; weight 0.33.
16. Imbricated ML: (1) consistent; (2) flaring periodically (*e. g.* *Lophospira serrulata*).
17. SK prominence [not equal to strength, as prominence refers to whole structure projecting from rest of shell; sometimes coincides with channel underneath peripheral band; however, species with channels and non-prominent peripheral bands and species with prominent peripheral bands and no obvious channel are both known]: (1) peripheral band not altering profile of whorl; (2) whole peripheral band projecting slightly, creating slight ridges between shell and peripheral band; (3) whole peripheral band projecting strongly, creating strong ridges between shell and peripheral band. Ordered; weight 0.5.
18. Slit: (1) absent; (2) present. Weight 1.
19. Slit depth: (1) shallow (extending <10° behind aperture, measured looking down coiling axis); (2) deep (extending ~20° behind aperture). Weight 1.
20. Maintenance of slit: (1) periodically erased or reduced, with shell material deposited within slit less frequently than on rest of shell, resulting in slit depth (and sometimes presence/absence) varying over time (*e. g.* *Trochonebella*; recognized in part by greater distance between lunulae than observed between growth lines); (2) continuously maintained (*e. g.* "*Schizolopha*" *moorei*). Weight 1.
21. Lunulae shape [lunulae here are growth lines within sinus keel]: (1) concentric (shallow U-shape); (4) V-shaped (*e. g.* *Lophospira centralis* and relatives). Weight 1.
22. Lunulae strength: (1) weaker than GLs; (2) same as GLs; (3) stronger than GLs (*i. e.* imbricated; *e. g.* *Trochonebella* spp.). Unordered; weight 1.
23. Imbricated lunulae type: (1) deep and obtuse; (2) serrated. Weight 1.
24. Ontogenetic change in imbricated lunulae: (1) juvenile whorls only; (2) throughout. Weight 1.
25. Reduction to monolineate SK over ontogeny: (1) absent; (2) monolineate on final whorls. Weight 1.
26. Peripheral band attitude: (1) projecting straight from shell, as seen on most species; (2) curving adapically, *e. g.* *Arjamannia* and relatives. Weight 1.
27. Midwhorl (MW) channel [groove underneath medial lira; often but not always associated with prominent band, and so coded separately]: (1) absent; (2) present. Weight 1.
28. MW channel strength: (1) weak; (2) strong. Weight 1.
29. SK position [described relative to aperture centroid, with 90(indicating that a plane is passing through centroid and that SK is perpendicular to coiling axis; 0(indicating that plane is parallel to coiling axis): (2) ~100°; (3) ~90°; (4) ~80°; (5) ~70°; (6) ~60°; (7) ~50°. Ordered; weight 0.2.
30. Ramp shape symmetry [on primitive bilaterally symmetrical gastropods, right and left ramp shapes are symmetrical; derived species are asymmetrical]: (1) right rounder; (2) symmetrical; (3) left rounder. Unordered; weight 1.

31. Right ramp (RR) shape: (1) globular; (2) convex; (3) flat; (4) slightly concave; (5) concave. Ordered; weight 0.125 (reflecting both continuous nature and de-weighting for asymmetry).
32. RR and LR lengths [on primitive bilaterally symmetrical gastropods, right and left ramp lengths are equal; lophospirids with longer right and longer left ramps are known]: (1) longer RR; (2) equal lengths; (3) longer LR. Unordered; weight 1.
33. RR length [describing angle from "top" of ramp to sinus apex, based on triangle passing through aperture centroid]: (3) ~50°; (4) ~60°; (5) ~70°; (6) ~80°; (7) ~90°. Ordered; weight 0.25.
34. LR length [see character 33]: (3) ~50°; (4) ~60°; (5) ~70°; (6) ~80°; (7) ~90°. Ordered; weight 0.25.
35. RR:LR projection [ramp projection describing angle of "rise" of ramp from sinus keel, based on plane passing through SK and aperture centroid]: (1) RR projection higher; (2) LR and RR projections equal. Weight 1.
36. RR projection [see character 35]: (5) ~60°; (6) ~70°; (7) ~80°. Ordered; weight 0.25.
37. LR projection [see character 35]: (3) ~40°; (4) ~50°; (5) ~60°; (6) ~70°; (7) ~80°. Ordered; weight 0.125.
38. Sutural carina (SC): (1) absent; (2) present. Weight 1.
39. SC strength: (1) weak (creating only a weak profile); (2) moderate (partly filling up the suture).
40. RR carina (RRC) [strong carina usually located at top of sinus]: (1) absent; (2) present. Weight 1.
41. RRC strength: (1) weak (creating no profile); (2) moderate (roughly equal to weak-to-moderate peripheral band); (3) strong (roughly equal to strong peripheral band). Ordered; weight 0.5.
42. RRC type: (2) thin local thickening; (3) round profile; (4) sharp profile. Unordered; weight 1.
43. Ontogenetic change in RRC strength: (1) absent; (2) becoming weaker on adult whorls. Weight 1.
44. Channel beneath RC: (1) absent; (2) present. Weight 1.
45. RRC location: (1) ~75° toward suture from SK; (2) ~45° toward suture from SK. Weight 1.
46. RRC attitude: (1) carina projecting perpendicularly to RR; (2) carina curving abapically. Weight 1.
47. RRC: (1) plain thread; (2) serrated. Weight 1.
48. Shape of shell at top of right ramp [usually at suture]: (1) oblique; (2) acute, with channel underneath suture. Weight 1.
49. LR shape [see character 31]: (1) globular; (2) very convex; (3) slightly convex; (4) flat. Ordered; weight 0.167.
50. Swelling at intersection of left ramp and base [might be primitively homologous with left ramp carina (character 51), and present on earliest gastropods]: (1) absent; (2) present. Weight 1.
51. LR carina (LRC): (1) absent; (2) present. Weight 1.
52. LRC type: (1) thick contusion, but creating more distinct profile than simple swelling; (2) sharp profile. Weight 1.
53. LRC strength [see character 41]: (1) weak; (2) moderate (~ sinus); (3) strong. Ordered; weight 1.
54. LRC [see character 47; species with serrated right carinae but plain left carina exist, indicating that the two evolve independently]: (1) plain thread; (2) serrated. Weight 1.
55. Second LRC: (1) one carina; (2) two carinae (*e. g. Lophospira quadrisulcata*). Weight 1.
56. Channel beneath LRC [see character 44]: (1) absent; (2) present. Weight 1.
57. Columella thickness: (1) no thicker than rest of shell; (2) slightly thicker than rest of shell; (3) much thicker (partly filling umbilicus); (4) extremely thick (filling umbilicus). Ordered; weight 0.33.
58. Umbilical carina (UC) [carina at base of shell, circling umbilicus]: (1) absent; (2) present. Weight 1.
59. UC type: (1) thick, dull protrusion; (2) sharp extension accommodating a channel; (3) lirum with sharp profile. Unordered; weight 1.
60. UC strength [see characters 41 and 53]: (1) very weak; (2) weak; (3) strong. Ordered; weight 0.5.
61. Ontogenetic change in UC strength: (1) constant; (2) becoming weaker on adult whorls. Weight 1.
62. UC location [with larger angle indicating UC closer to coiling axis]: (1) ~120° below SK; (2) ~90° below SK. Weight 1.
63. Angle at base of columella [narrower angle indicates sharper, more siphonate base of shell]: (3) ~60°; (4) ~75°; (5) ~90°; (6) ~105°; (7) ~120°. Ordered; weight 0.25.
64. Shape of columella on inner margin [can differ from shape on outer margin, so the two coded separately]: (1) arching like half-circle; (2) arching in obtuse curve; (3) trending toward straight; (4) curving slightly into the aperture. Ordered; weight 0.5.
65. Outer margin shape: (1) more obtuse than inner margin; (2) same as inner margin; (3) more acute than inner margin. Weight 1.
66. Ontogenetic change in margin shape: (1) none; (2) becoming rounder over ontogeny. Weight 1.
67. Columella attitude [describing main trend of columella relative to coiling axis]: (1) 0° (*i. e.* perpendicular to coiling axis); (2) 15°; (3) 30°; (4) 45°; (5) 60°. Ordered; weight 0.25.
68. Columella lira [carina in middle of columella, visible in umbilicus]: (1) absent; (2) present. Weight 1.
69. Parietal inductura thickness [silicification can occur differently among different shell layers, which can affect characters such as this; therefore, "relative" states were coded based on comparisons among taxa found from the same beds, with comparisons among conspecifics from different beds used to establish the final character code]: (1) absent; (2) thinner than rest of shell; (3) thickness same as shell. Unordered; weight 1.
70. Columella reflected around coiling axis: (1) absent; (2) present. Weight 1.
71. Whole aperture inclined (tangential): (1) absent; (2) present. Weight 1.
72. Degree of whole aperture inclination (InAn): (1) ~10°; (2) ~20°; (3) ~30°; (4) ~40°; (5) ~50°; (6) ~60°. Ordered; weight 0.2.
73. Left side of aperture only inclined [or inclined at different angle than right side]: (1) absent; (2) present. Weight 1.
74. Left InAn: (1) ~10°; (2) ~20°; (3) ~30°. Ordered; weight 0.5.
75. Right side of aperture only inclined [or inclined at different angle than left side]: (1) absent; (2) present. Weight 1.
76. Right InAn: (1) ~10°; (2) ~20°; (3) ~30°. Ordered; weight 0.5.
77. Anterior projection of aperture [best observed from base, because growth lines will project forward instead of radially; it is important that they do this at the onset, as tangential aperture will cause growth lines on the periphery to slope forward as well]: (1) absent; (2) present. Weight 1.
78. Degree of anterior projection [relative to plane passing radially through coiling axis]: (1) 10°; (2) 20°; (3) 30°; (4) 40°; (5) 50°. Ordered; weight 0.25.
79. Aperture expansion [expansion of shell in radians as a "tube"]: (2) 0.05-0.10; (3) 0.10-0.15; (4) 0.15-0.20. Ordered; weight 0.5.
80. Curvature about coiling axis [in radians]: (3) 0.65 < K < 0.75; (4) 0.75 < K < 0.85; (5) 0.85 < K < 0.95. Ordered; weight 0.5.
81. Translation (T) [vector of downwards growth (in radians)]: (5) 0.16 < T < 0.47 (low dextral); (6) 0.47 < T < 0.79 (moderate dextral); (7) 0.79 < T < 1.10 (high dextral); (8) 1.10 < T < 1.41 (very high dextral). Ordered; weight 0.33.
82. Continuous ontogenetic change in T: (2) isometric; (3) continuously increasing, resulting in ever-increasing apical angle. Weight 1.
83. Early ontogenetic change in T: (1) early decrease of T (*e. g. Trochonema, Trochonemella*); (2) isometric; (3) early increase in T. Unordered; weight 1.

- 84. Late ontogenetic change in T [often resulting in open-coiled "cork-screw"-like shells, e. g. *Lophospira helicteres*, *Eunema strigillata*]: (2) isometric; (3) late increase in T. Weight 1.
- 85. Punctuated late ontogenetic change in T: (1) occurring over 1-2 whorls (e. g. *Trochonema*, *Trochonemella*); (2) punctuated, occurring over less than one revolution. Weight 1.
- 86. Magnitude of late ontogenetic change in T: (1) slight, changing suture point; (2) major, resulting in open coiling. Weight 1.
- 87. Ornament on left side of aperture: (1) absent; (2) present on left ramp and base; (3) present on left ramp only. Unordered; weight 0.5.
- 88. LR ornament density [based on average angular distance between threads]: (1) 1 per 20°; (2) 1 per 10°; (3) 1 per 5°; (4) 1 per 1°. Ordered; weight 0.5.
- 89. LR ornament type: (1) thin local thickenings, little stronger than growth lines and with no profile (e. g. *Ruedemannia*); (2) lirae with weak profile (e. g. *Arjamannia*); (3) thick lirae with strong profile (e. g. *Longstaffia*). Weight 1.
- 90. RR ornament [because species with left ramp ornament sometimes lack right ramp ornament, these characters coded separately; completely inornate to completely ornate represents one step]: (1) absent; (2) present. Weight 0.5.
- 91. RR ornament density [see character 88]: (1) 1 per 20°; (2) 1 per 10°; (3) 1 per 5°; (4) 1 per 1°. Ordered; weight 0.5.
- 92. RR ornament strength: (1) thin threads; (2) weak lirae; (3) strong lirae. Ordered; weight 0.5.
- 93. Ornament as changes in aperture shape: (1) simple local thickenings of shell; (2) representing local flarings of aperture. Weight 1.
- 94. Ontogenetic change in RR ornament: (1) constant; (2) weaker on adult whorls. Weight 1.
- 95. Size: (1) <10 mm³ (micro-mollusk); (2) small (>10 to <10² mm³); (3) moderate (>10² to <10³ mm³); (4) large (>10³ to <10⁴ mm³). Ordered; weight 0.33.

APPENDIX 2
CHARACTER MATRIX

Character data for lophospiroid species. See Appendix 1 for characters and character descriptions. [?, characters that could not be observed; -, characters that do not pertain to a species (e. g. ornament type for an inornate species); A-D denote polymorphic species [A, states 1 + 2; B, states 1 + 3; C, states 2 + 3; D, states 6 + 7]; BMNH, The Natural History Museum, London].

Species	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Ø <i>Hormotoma simulatrix</i> (Billings, 1865)	2	5	3	3	1	1	2	1	4	2	2	3	1	-	?
Ø <i>Ectomaria adelina</i> (Billings, 1865)	2	5	3	3	1	1	2	1	6	2	2	3	1	-	?
1 <i>Pagodospira cicelia</i> (Billings, 1865)	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2
2 <i>Lophospira perangulata</i> (Hall, 1847)	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2
3 <i>L. sorrorcula</i> (Billings, 1865)	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2
4 <i>L. rectistriata</i> (Billings, 1865)	2	4	2	3	1	1	2	1	2	2	2	3	2	2	2
5 <i>Pagodospira derwiduii</i> Grabau, 1922	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2
6 <i>Lophospira milleri</i> (Hall in Miller, 1889)	2	4	2	3	1	1	3	1	2	2	2	3	2	2	2
7 <i>Trochonemella knoxvillensis</i> Ulrich in Ulrich and Scofield, 1897	2	5	3	3	1	1	4	1	2	2	2	3	2	2	2
8 <i>Proturritella bicarinata</i> (Koken, 1889)	2	4	2	3	1	1	3	1	2	1	-	-	2	2	3
9 <i>Pagodospira dorothea</i> Grabau, 1922	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2
10 <i>Trochonemella trochonemoides</i> (Ulrich in Ulrich and Scofield, 1897)	2	5	2	3	1	2	3	1	2	1	-	-	2	2	3
11 <i>Lophospira centralis</i> Ulrich and Scofield, 1897	2	3	2	2	1	1	3	1	2	2	2	3	2	2	2
12 <i>Trochonema bellula</i> Ulrich and Scofield, 1897	2	4	2	3	1	2	3	1	1	1	-	-	2	2	3
13 <i>T. eccentrica</i> Ulrich and Scofield, 1897	2	3	2	2	1	2	3	1	1	1	-	-	2	2	3
14 <i>Trochonemella montrealensis</i> Okulitch, 1935	2	4	1	3	1	2	4	1	2	2	2	3	1	-	-
15 <i>Lophospira helicteres</i> (Salter, 1859)	2	3	2	2	1	1	3	1	2	2	2	3	2	2	3
16 <i>Trochonemella</i> n. sp.	2	4	1	3	1	2	4	1	2	2	2	3	1	-	-
17 <i>Lophospira serrulata</i> (Salter, 1859)	2	5	3	3	1	1	4	1	2	2	2	3	2	2	3
18 <i>Eunema strigillata</i> Salter, 1859	2	3	2	2	1	1	3	1	1	1	-	-	2	2	3
19 <i>Trochonema umbilicata</i> (Hall, 1847)	2	3	2	2	1	2	3	1	1	1	-	-	2	2	3
20 <i>T. canadensis</i> Wilson, 1951	2	3	1	2	1	2	3	1	1	1	-	-	2	2	3
21 <i>T. wilsoni</i> Steele and Sinclair, 1971	2	3	2	2	1	2	3	1	1	1	-	-	2	2	3
22 <i>Lophospira ventricosa</i> (Salter, 1859)	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2
23 <i>Trochonemella notabilis</i> (Ulrich in Ulrich and Scofield, 1897)	2	4	1	3	1	2	4	1	2	2	2	3	1	-	-
24 <i>Gyronema pulchella</i> Ulrich and Scofield, 1897	2	3	1	2	1	1	2	1	1	1	-	-	2	2	2
25 <i>G. semicarinata</i> (Ulrich and Scofield, 1897)	2	3	1	2	1	1	2	1	1	1	-	-	2	2	2
26 <i>G. liljevalli</i> Rohr, 1980	2	3	2	2	1	2	3	1	1	1	-	-	2	2	3
27 <i>Trochonema madisonense</i> Ulrich and Scofield, 1897	2	4	2	3	1	2	3	1	1	1	-	-	2	2	3
28 <i>Lophospira burginensis</i> Ulrich and Scofield, 1897	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2
29 <i>L. oweni</i> Ulrich and Scofield, 1897	2	5	3	3	1	1	2	1	2	2	2	3	2	2	1
30 <i>L. concinula</i> Ulrich and Scofield, 1897	2	3	1	2	1	1	3	1	2	2	2	3	2	2	3
31 <i>L. spironema</i> Ulrich and Scofield, 1897	2	4	2	3	1	1	3	1	2	2	2	3	2	2	2
32 <i>Donaldiella decursa</i> (Ulrich and Scofield, 1897)	2	5	3	3	1	1	2	1	2	2	1	3	2	2	2
33 <i>D. conoidea</i> (Ulrich and Scofield, 1897)	2	5	3	3	1	1	2	1	2	2	1	3	2	2	1
34 <i>D. producta</i> (Ulrich and Scofield, 1897)	2	5	3	3	1	1	2	1	2	2	1	2	2	2	2
35 <i>D. Curdsville</i> sp.	2	5	3	3	1	1	2	1	2	2	1	2	2	2	2
36 <i>Lophospira sumnerensis</i> (Safford, 1869)	2	5	3	3	1	1	2	1	2	2	2	3	2	2	1
37 <i>Trochonema salteri</i> Ulrich and Scofield, 1897	2	3	2	2	1	2	3	1	1	1	-	-	2	2	3
38 <i>Ruedemannia humilis</i> (Ulrich and Scofield, 1897)	2	4	2	3	1	1	2	1	4	2	2	2	2	1	2
39 <i>R. lirata</i> (Ulrich and Scofield, 1897)	2	4	2	3	1	1	2	1	4	2	2	2	2	1	2
40 <i>Lophospira tenuistriata</i> Ulrich and Scofield, 1897	2	5	3	3	1	1	2	1	2	2	2	3	2	2	2

(continued)

APPENDIX 2. (continued)

25	<i>G. semicarinata</i>	1	2	1	-	-	4	2	-	-	-	1	2	1	3	2	3	3	3	4	1	5	3	1	-	2	2	3	1	1	2	1	1	1	3	1	2	2	2	1	2		
26	<i>G. liljevalli</i>	1	2	1	-	-	1	2	-	-	-	1	2	2	7	1	2	2	7	7	1	7	5	2	2	2	2	3	1	2	2	1	1	1	3	1	2	2	2	1	2		
27	<i>T. madisonense</i>	1	2	1	-	-	1	2	-	-	-	1	2	2	7	2	3	2	7	7	1	7	5	2	2	2	3	3	1	2	2	1	1	1	3	1	2	2	2	1	1		
28	<i>L. buriginensis</i>	1	2	1	-	-	1	2	-	-	-	1	2	1	3	3	3	2	3	3	1	5	3	1	-	2	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1		
29	<i>L. oweni</i>	1	3	1	-	-	1	2	-	-	-	2	1	2	1	3	3	3	2	3	3	1	5	3	1	-	2	1	1	2	1	1	1	1	1	2	2	2	1	1	1	1	
30	<i>L. concinula</i>	1	2	1	-	-	4	2	-	-	-	1	2	1	3	2	3	3	3	4	1	5	3	2	1	2	3	3	1	2	1	1	1	1	3	1	2	2	2	1	1		
31	<i>L. spironema</i>	1	2	1	-	-	1	2	-	-	-	1	2	1	3	3	4	3	3	4	1	5	3	1	-	2	2	3	1	1	1	1	1	1	3	1	2	2	2	1	1		
32	<i>D. decursa</i>	1	2	1	-	-	1	2	-	-	-	1	2	1	2	1	5	2	3	3	1	5	3	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
33	<i>D. conoidea</i>	1	2	1	-	-	1	2	-	-	-	1	2	1	2	2	3	2	3	3	1	5	3	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
34	<i>D. producta</i>	1	2	1	-	-	1	2	-	-	-	1	2	1	2	1	4	2	3	3	1	5	3	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
35	<i>D. Curdsville sp.</i>	1	2	1	-	-	1	2	-	-	-	1	2	1	2	1	4	2	3	3	1	5	3	1	-	2	1	1	1	1	1	1	1	1	3	2	2	1	1	1	1	1	
36	<i>L. sumnerensis</i>	1	3	1	-	-	1	2	-	-	-	2	1	2	1	6	3	5	1	5	3	1	7	4	2	2	2	1	1	2	1	1	1	1	2	2	1	-	-	-	-	-	
37	<i>T. salteri</i>	1	2	1	-	-	1	2	-	-	-	1	2	2	4	2	3	1	5	4	1	6	5	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
38	<i>R. humilis</i>	1	1	1	-	-	1	2	-	-	-	1	2	1	3	1	2	1	5	4	1	5	3	1	-	2	2	3	1	1	2	1	1	1	2	?	2	2	1	1	1	1	
39	<i>R. lirata</i>	1	1	1	-	-	1	2	-	-	-	1	2	1	3	1	2	1	5	4	1	5	3	1	-	2	2	3	1	1	2	1	1	1	2	?	2	2	1	1	1	1	
40	<i>L. tenuistriata</i>	1	2	1	-	-	1	2	-	-	-	1	2	1	3	3	2	3	3	1	5	3	1	-	2	1	3	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	
41	<i>L. tropidophora</i>	1	3	1	-	-	1	2	-	-	-	2	1	2	1	3	3	3	2	3	3	1	5	3	1	-	2	1	1	2	1	1	1	1	2	2	2	1	1	1	1	1	1
42	<i>D. filosa</i>	1	3	1	-	-	1	2	-	-	-	1	2	1	3	3	5	2	3	3	1	5	3	1	-	1	1	1	1	1	1	1	1	2	2	1	-	-	-	-	-	-	
43	<i>D. bowdeni</i>	1	3	1	-	-	1	2	-	-	-	2	1	2	1	3	3	2	3	3	1	5	3	1	-	2	1	1	2	1	1	1	1	2	2	2	1	1	1	1	1	1	
44	<i>L. bellicarinata</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	4	3	5	3	3	7	1	6	4	2	2	2	2	3	1	1	2	1	1	2	3	1	2	1	2	1	2	1	1
45	<i>L. quadrisulcata</i>	1	2	1	-	-	4	2	-	-	-	1	2	1	3	3	4	3	3	4	1	5	3	2	1	2	3	3	1	2	1	1	1	1	3	1	2	2	2	1	2		
46	<i>L. moorei</i>	1	3	2	2	1	4	2	-	-	-	2	1	2	1	3	3	2	3	3	1	5	3	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
47	<i>L. aff. L. serrulata</i>	?	2	2	1	1	1	3	2	2	-	1	2	1	5	1	4	2	7	7	1	7	6	1	-	2	3	3	1	1	2	2	2	1	3	1	2	2	3	2	1	1	
48	<i>T. BMNH 36364</i>	?	2	2	1	1	1	3	2	2	-	1	2	1	5	1	4	2	7	7	1	7	6	1	-	2	3	3	1	1	2	2	2	1	3	1	2	2	3	2	2	2	
49	<i>T. churkini</i>	1	2	2	1	1	1	3	1	2	1	1	2	2	6	1	2	2	7	7	1	7	6	1	-	2	3	3	1	1	2	2	2	1	3	1	2	2	3	1	1	1	
50	<i>T. reusingi</i>	1	2	2	1	1	1	3	1	2	1	1	2	2	6	1	2	2	7	7	1	7	6	1	-	2	3	3	1	1	2	2	2	1	3	1	2	2	3	2	1	1	
51	<i>T. aff. umbilicata</i>	1	2	1	-	-	1	2	-	-	-	1	2	2	4	2	3	2	7	7	1	6	5	2	2	2	2	3	1	2	2	1	1	1	3	1	2	2	3	1	1	1	
52	<i>A. thraivensis</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	4	3	4	3	3	7	1	6	4	2	2	2	2	3	1	1	2	1	1	2	3	1	2	1	2	1	1	1	
53	<i>G. bicarinata</i>	1	3	1	-	-	1	2	-	-	-	1	2	2	4	2	3	1	5	4	2	6	6	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
54	<i>L. ?borkholmensis</i>	1	1	1	-	-	1	2	-	-	-	1	2	1	3	1	2	1	5	4	1	5	3	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
55	<i>T. pandori</i>	1	2	1	-	-	1	2	-	-	-	1	2	2	7	2	3	2	7	7	1	7	5	2	2	2	3	3	1	2	2	1	1	3	1	2	2	2	1	1	1	1	
56	<i>T. aff. pandori</i>	1	2	1	-	-	1	2	-	-	-	1	2	2	7	2	3	2	7	7	1	7	5	2	1	2	3	3	1	2	1	1	1	1	3	1	2	2	2	1	1	1	
57	<i>L. sedgewicki</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	4	3	5	3	5	7	1	6	4	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
58	<i>L. ?hyaacinthisis</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	4	3	5	3	5	7	1	6	4	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
59	<i>L. centervillensis</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	3	3	3	3	4	6	1	6	4	1	-	2	2	3	1	1	2	1	1	1	1	2	2	2	1	1	1	1	
60	<i>A. cancellata</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	4	3	3	3	3	7	1	6	4	2	2	2	2	3	1	1	2	1	1	2	3	1	2	1	1	1	1	1	1
61	<i>A. woodlandi</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	4	2	3	3	3	7	1	6	4	2	2	?	?	?	?	1	1	1	1	2	3	1	2	1	1	1	1	1	1
62	<i>D. trilineata</i>	1	3	1	-	-	1	2	-	-	-	1	2	1	3	3	3	2	3	3	1	5	3	1	-	?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
63	<i>L. gotlandica</i>	1	3	1	-	-	4	2	-	-	-	2	2	1	6	3	5	3	5	7	1	6	4	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
64	<i>L. laquetta</i>	1	2	1	-	-	1	2	-	-	-	2	2	1	3	1	2	3	4	6	1	6	5	1	-	2	2	3	1	1	2	1	1	1	1	1	2	2	2	1	1	1	
65	<i>A. inexpectans</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	4	2	3	3	3	7	1	6	4	2	2	2	2	2	1	2	1	1	1	2	3	1	2	1	2	1	1	1	1
66	<i>L. holmi</i>	1	3	1	-	-	1	2	-	-	-	2	2	1	3	3	2	1	5	4	1	5	3	1	-	2	2	3	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1
67	<i>K. nelsonae</i>	1	3	1	-	-	4	2	-	-	-	2	2	1	6	3	5	3	5	7	1	6	4	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
68	<i>L. munda</i>	2	3	1	-	-	1	3	2	2	-	2	2	1	4	3	3	1	5	3	1	6	4	2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
69	<i>L. imbricata</i>	2	3	1	-	-	1	3	2	2	-	2	2	1	4	2	3	1	5	3	1	6	4	2	2	1	-	2	2	3	1	1	1	1	2	2	1	1	1	1	1	1	1
70	<i>T. turrita</i>	1	3	1	-	-	1	2	-	-	-	1	2	2	3	1	2	2	7	7	2	7	7	2	2	2	2	3	1	1	2	1	1	1	2	1	2	2	2	2	1	1	1
71	<i>E. kayesi</i>	1	3	1	-	-	1	2	-	-	-	1	2	2	3	1	2	2	7	7	2	7	7	2	2	2	2	3															

APPENDIX 2. (continued)

9	<i>P. dorothea</i>	-	?	1	-	-	-	?	2	3	2	1	1	1	3	?	1	-	1	-	1	-	1	-	1	-	2	5	8	3	2	2	-	-	1	-	-	1	-	-	-	-	1		
10	<i>T. trochonemoides</i>	2	1	2	3	2	2	2	4	2	2	1	5	1	4	1	2	3	1	-	1	-	2	3	4	4	5	3	1	3	1	1	1	1	-	-	1	-	-	1	-	-	-	-	2
11	<i>L. centralis</i>	1	2	1	-	-	-	?	4	3	2	1	2	1	3	2	1	-	2	3	1	-	1	-	1	-	3	6	6	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	1
12	<i>T. bellula</i>	2	1	2	3	2	1	2	5	2	2	1	5	1	4	1	2	5	1	-	1	-	2	3	4	4	5	3	1	3	1	1	1	1	-	-	1	-	-	-	-	-	-	-	2
13	<i>T. eccentrica</i>	2	1	2	3	2	1	2	5	2	2	1	5	2	4	1	2	6	1	-	1	-	2	4	4	4	5	3	1	3	-	1	1	-	-	1	-	-	-	-	-	-	-	2	
14	<i>T. montrealensis</i>	2	2	2	1	1	1	4	2	2	1	4	1	4	1	4	2	3	1	-	1	-	2	3	4	4	5	3	1	3	1	1	1	1	-	-	1	-	-	-	-	-	-	-	2
15	<i>L. helicteres</i>	2	2	2	1	1	2	2	4	2	2	2	2	1	4	2	1	-	2	2	1	-	1	-	1	-	3	6	D	3	3	3	2	2	1	-	-	1	-	-	-	-	-	-	2
16	<i>T. n. sp.</i>	2	2	2	1	1	1	1	5	2	2	1	4	1	4	1	2	4	1	-	1	-	2	2	4	4	5	3	1	3	1	2	1	-	-	1	-	-	-	-	-	-	-	2	
17	<i>L. serrulata</i>	1	2	2	1	1	1	2	2	3	2	1	1	1	3	2	1	-	1	-	1	-	1	-	2	5	D	3	3	3	2	2	1	-	-	1	-	-	-	-	-	-	-	1	
18	<i>E. strigillata</i>	2	2	2	1	1	2	2	4	3	2	2	2	1	4	2	1	-	1	-	1	-	1	-	3	6	D	3	2	3	2	2	1	-	-	1	-	-	-	-	-	-	-	2	
19	<i>T. umbilicata</i>	2	1	2	3	2	1	1	6	1	2	1	5	2	4	1	2	6	1	-	1	-	2	4	4	4	5	3	1	3	-	1	1	-	-	1	-	-	-	-	-	-	-	2	
20	<i>T. canadensis</i>	2	1	2	3	2	1	1	6	1	2	1	5	2	4	1	2	6	1	-	1	-	2	4	4	4	5	3	1	3	-	1	1	-	-	1	-	-	-	-	-	-	-	2	
21	<i>T. wilsoni</i>	2	1	2	3	2	1	1	6	1	2	1	5	2	4	1	2	6	1	-	1	-	2	4	4	4	5	3	1	3	-	1	1	-	-	1	-	-	-	-	-	-	-	2	
22	<i>L. ventricosa</i>	-	2	1	-	-	-	?	2	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	3	5	7	3	3	2	-	1	1	-	-	1	-	-	-	-	-	-	-	1	
23	<i>T. notabilis</i>	2	2	2	1	1	1	1	5	2	2	1	3	1	4	1	2	4	1	-	1	-	2	4	4	4	5	3	1	3	1	2	1	-	-	1	-	-	-	-	-	-	-	2	
24	<i>G. pulchella</i>	1	2	?	-	-	-	?	4	3	2	1	2	1	3	2	1	-	2	3	1	-	1	-	3	6	6	3	2	2	-	-	2	3	1	-	-	-	-	-	-	-	-	1	
25	<i>G. semicarinata</i>	1	2	?	-	-	-	?	4	3	2	1	2	1	3	2	1	-	2	3	1	-	1	-	3	6	6	3	2	2	-	-	2	2	3	2	2	3	1	1	1	1	1	1	1
26	<i>G. liljevalli</i>	2	1	1	-	-	-	?	6	1	2	1	5	2	4	1	2	6	1	-	1	-	2	5	4	4	5	3	1	3	-	1	1	-	-	1	-	-	-	-	-	-	-	1	
27	<i>T. madisonense</i>	2	1	2	3	2	1	2	6	2	2	1	5	1	4	1	2	6	1	-	1	-	2	3	4	4	5	3	1	3	-	1	1	-	-	1	-	-	-	-	-	-	3		
28	<i>L. burginensis</i>	1	3	1	-	-	-	?	3	3	1	1	1	1	3	1	1	-	1	-	1	-	1	-	3	5	6	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	1	
29	<i>L. oweni</i>	1	4	1	-	-	-	?	3	3	1	1	2	1	3	1	1	-	1	-	1	-	1	-	3	5	6	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	2	
30	<i>L. concinula</i>	2	2	2	3	1	2	2	4	3	2	1	2	1	4	2	1	-	2	1	2	1	1	-	3	6	6	3	2	3	1	1	1	-	-	1	-	-	-	-	-	-	-	1	
31	<i>L. spironeuma</i>	1	2	1	-	-	-	?	4	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	3	6	6	3	2	2	-	-	2	4	1	1	-	-	-	-	-	-	-	1	
32	<i>D. decursa</i>	1	2	1	-	-	-	?	2	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	2	5	7	3	2	2	-	1	1	-	-	1	-	-	-	-	-	-	-	1	
33	<i>D. conoidea</i>	1	2	1	-	-	-	?	2	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	2	5	7	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	2	
34	<i>D. producta</i>	1	2	1	-	-	-	?	2	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	2	5	8	3	2	3	1	1	1	-	-	1	-	-	-	-	-	-	-	2	
35	<i>D. Curdsville sp.</i>	1	2	1	-	-	-	?	2	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	2	5	8	3	2	3	2	2	1	-	-	1	-	-	-	-	-	-	-	2	
36	<i>L. summerensis</i>	-	4	1	-	-	-	?	3	3	1	1	2	1	3	1	2	3	1	-	1	-	1	-	3	6	7	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	2	
37	<i>T. salteri</i>	-	1	2	3	2	1	1	6	1	2	1	3	1	4	1	1	-	1	-	1	-	2	1	3	5	6	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	2	
38	<i>R. humilis</i>	1	2	1	-	-	-	?	4	2	2	1	2	1	3	2	1	-	1	-	1	-	1	-	4	6	6	2	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	1	
39	<i>R. lirata</i>	1	2	1	-	-	-	?	4	2	2	1	2	1	3	2	1	-	1	-	1	-	1	-	4	6	6	2	2	2	-	-	2	4	1	1	-	-	-	-	-	-	-	1	
40	<i>L. tenuistriata</i>	1	3	1	-	-	-	?	3	3	1	1	1	1	3	?	1	-	1	-	1	-	1	-	3	5	7	3	2	2	-	-	2	3	1	2	3	1	1	1	1	1	1	1	1
41	<i>L. tropidophora</i>	1	4	1	-	-	-	?	3	3	1	1	2	1	3	1	1	-	1	-	1	-	1	-	3	5	6	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	2	
42	<i>D. filosa</i>	-	2	1	-	-	-	?	2	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	2	5	8	3	2	2	-	-	1	1	-	-	1	-	-	-	-	-	-	1	
43	<i>D. bowdeni</i>	1	3	1	-	-	-	?	4	3	2	1	2	1	3	2	1	-	1	-	1	-	1	-	2	5	8	3	2	2	1	1	1	-	-	1	-	-	-	-	-	-	-	2	
44	<i>L. bellicarinata</i>	1	2	1	-	-	-	?	4	3	2	1	2	1	3	2	1	-	1	-	2	1	1	-	3	6	7	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	2	
45	<i>L. quadrisculcata</i>	2	2	2	3	1	2	2	4	3	2	1	2	1	4	2	1	-	2	1	2	1	1	-	3	6	6	3	2	3	1	1	1	-	-	1	-	-	-	-	-	-	-	2	
46	<i>L. moorei</i>	-	?	1	-	-	-	?	3	3	1	1	2	1	?	?	1	-	1	-	1	-	1	-	3	5	6	3	2	2	-	-	1	-	-	1	-	-	-	-	-	-	-	2	
47	<i>L. aff. serrulata</i>	2	2	2	3	1	1	2	4	3	2	1	2	1	3	1	2	1	1	-	2	1	1	-	2	1	3	5	6	3	2	3	1	1	1	-	-	1	-	-	-	-	-	1	
48	<i>T. BMNH 36364</i>	2	2	2	3	1	1	2	4	2	2	1	2	1	3	1	2	1	1	-	2	1	2	2	3	5	6	3	2	3	1	1	1	-	-	1	-	-	-	-	-	-	-	2	
49	<i>T. churkini</i>	2	2	2	1	1	1	1	5	2	2	1	3	1	4	1	2	5	1	-	2	1	2	2	4	4	6	3	2	3	1	2	1	-	-	1	-	-	-	-	-	-	-	2	
50	<i>T. reusingi</i>	2	2	2	1	1	1	1	5	2	2	1	3	1	4	1	2	5	1	-	2	1	2	2	4	4	6	3	2	3	1	2	1	-	-	1	-	-	-	-	-	-	-	2	
51	<i>T. aff. umbilicata</i>	1	1	2	3	2	1	1	6	1	2	1	4	1	4	1	2	2	1	-	1	-	2	2	3	5	6	3	1	2	-	-	1	1	-	-	1	-	-	-	-	-	-	2	
52	<i>A. thraivensis</i>	1	2	1	-	-	-	?	4	3	2	1	2	1	3	2	1	-	1	-	2	2	1	-	3	6	7	3	2	2	1	1	2	3	3	1	-	-	-	-	-	-	-	2	
53	<i>G. bicarinata</i>	-	1	2	2	3	1	2	6	3	2	1	3	1	4	1	1	-	1	-	1	-	2	1	3	6	6	3	2	3	-	1	1	-	-	1	-	-	-	-	-	-	-	2	
54	<i>L. ?borkholmensis</i>	1	?	1	-	-	-	?	4	1	2	1	4	1	?	?	1	-																											

APPENDIX 3
STRATIGRAPHIC DATA

Range and sampling data for lophospiroid species. Separate horizon scales are used for each realm when calculating the likelihood of gaps (Wagner, 1995a). Stratigraphic debt and discrete ranges were calculated using the scales on Fig. 1, where Cassinian = Middle Arenig, Fennian = Late Arenig, Llanvirn = Early Llanvirn, Llandeilo = Late Llanvirn, Ashbian-Black Riveran = Early Caradoc, Rocklandian-Kirkfieldian = Middle1 Caradoc, Shermanian-Edenian = Middle2 Caradoc, Maysvillian-Richmondian = Ashgill, Rhuddanian-Aeronian = Early Llandovery, Telychian = Late Llandovery, Sheinwoodian = Early Wenlock, Homerian = Late Wenlock, Gorstian = Early Ludlow, and Ludfordian = Late Ludlow. [FKA, oldest sampled horizon, counted as number of older lophospiroid horizons known up to that point (see Wagner, 1995a); FSA, first stage from which a species is known; H, number of horizons from which a species is known; LKA, latest sampled horizons; LSA, last stage from which a species is known; Realm, biogeographic province: Baltica (Balt), Gondwana (Gond), Laurentia (Laur), Toquima-Tablehead (ToqTab)].

No. Species	H	FKA	LKA	Realm	FSA	LSA
1 <i>Pagodospira cicelia</i>	14	1	57	Laur	Cassinian	Llanvirn
2 <i>Lophospira perangulata</i>	85	1	256	Laur	Cassinian	Richmondian
3 <i>L. sorrorcula</i>	16	18	57	ToqTab	Fennian	Llandeilo
4 <i>L. rectistriata</i>	6	18	44	Laur	Fennian	Llandeilo
5 <i>Pagodospira derwiduii</i>	7	18	27	ToqTab	Fennian	Llanvirn
6 <i>Lophospira milleri</i>	49	18	256	Laur	Llanvirn	Richmondian
7 <i>Trochonemella knoxvillensis</i>	7	18	44	Laur	Llanvirn	Llandeilan
8 <i>Prourritella bicarinata</i>	19	22	48	Balt	Llandeilan	Llandeilan
9 <i>Pagodospira dorothea</i>	1	22	44	ToqTab	Llandeilo	Llandeilan
10 <i>Trochonemella trochonemoides</i>	5	22	46	Laur	Llandeilo	Ashby
11 <i>Lophospira centralis</i>	35	45	220	Laur	Ashby	Rocklandian
12 <i>Trochonema bellula</i>	1	45	46	Laur	Ashby	Black Riveran
13 <i>T. eccentrica</i>	1	45	47	Laur	BlackRiveran	Black Riveran
14 <i>Trochonemella montrealensis</i>	8	47	91	Laur	BlackRiveran	Black Riveran
15 <i>Lophospira helicteres</i>	16	47	131	Laur	BlackRiveran	Rocklandian
16 <i>Trochonemella</i> n. sp.	3	47	91	Laur	BlackRiveran	Black Riveran
17 <i>Lophospira serrulata</i>	16	47	137	Laur	BlackRiveran	Kirkfieldian
18 <i>Eunema strigillata</i>	5	47	131	Laur	BlackRiveran	Black Riveran
19 <i>Trochonema umbilicata</i>	31	47	203	Laur	BlackRiveran	Shermanian
20 <i>T. canadensis</i>	3	47	91	Laur	BlackRiveran	Shermanian
21 <i>T. wilsoni</i>	1	47	58	Laur	BlackRiveran	Shermanian
22 <i>L. ventricosa</i>	13	59	208	Laur	BlackRiveran	Kirkfieldian
23 <i>Trochonemella notabilis</i>	4	92	131	Laur	BlackRiveran	Black Riveran
24 <i>Gyronema semicarinata</i>	6	59	131	Laur	Rocklandian	Rocklandian
25 <i>G. pulchella</i>	4	92	137	Laur	BlackRiveran	Rocklandian
26 <i>G. liljevalli</i>	1	97	107	ToqTab	Rocklandian	Rocklandian
27 <i>Trochonema madisonense</i>	7	97	256	Laur	Kirkfieldian	Richmondian
28 <i>Lophospira burginensis</i>	13	97	209	Laur	Rocklandian	Edenian
29 <i>L. oweni</i>	11	119	209	Laur	Rocklandian	Edenian
30 <i>L. concinula</i>	4	132	165	Laur	Rocklandian	Rocklandian
31 <i>L. spironema</i>	2	132	137	Laur	Rocklandian	Rocklandian
32 <i>Donaldiella decursa</i>	1	155	184	Laur	Kirkfieldian	Shermanian
33 <i>D. conoidea</i>	1	155	165	Laur	Kirkfieldian	Shermanian
34 <i>D. producta</i>	1	155	165	Laur	Kirkfieldian	Shermanian
35 <i>D. Curdsville</i> sp.	1	187	208	Laur	Kirkfieldian	Shermanian
36 <i>Lophospira sumnerensis</i>	15	138	208	Laur	Shermanian	Richmondian
37 <i>Trochonema salteri</i>	8	138	265	Laur	Shermanian	Richmondian
38 <i>Ruedemannia humilis</i>	3	155	184	Laur	Edenian	Richmondian
39 <i>R. lirata</i>	6	187	253	Laur	Edenian	Richmondian
40 <i>Lophospira tenuistriata</i>	3	187	220	Laur	Edenian	Richmondian
41 <i>L. tropidophora</i>	29	187	256	Laur	Edenian	Richmondian
42 <i>D. filosa</i>	1	187	208	Laur	Edenian	Edenian
43 <i>D. bowdeni</i>	21	187	256	Laur	Edenian	Richmondian
44 <i>Lophospira bellicarinata</i>	2	210	256	Laur	Maysvillian	Richmondian
45 <i>L. quadrisulcata</i>	6	210	220	Laur	Maysvillian	Maysvillian
46 <i>L. moorei</i>	7	221	256	Laur	Richmondian	Richmondian
47 <i>L. aff. serrulata</i>	3	221	256	Laur	Richmondian	Richmondian
48 <i>Trochonemella</i> BMNH 36364	1	221	256	Laur	Richmondian	Richmondian
49 <i>T. churkini</i>	3	221	256	Laur	Richmondian	Richmondian

(continued)

APPENDIX 3. (continued)

50	<i>T. reusingi</i>	3	221	256	Laur	Richmondian	Richmondian
51	<i>Trochonema</i> aff. <i>umbilicata</i>	3	221	256	Laur	Richmondian	Richmondian
52	<i>Arjamannia sybellina</i>	5	221	256	Laur	Richmondian	Richmondian
53	<i>Globonema bicarinata</i>	2	223	239	Balt	Richmondian	Richmondian
54	<i>Lophospira</i> ? <i>borkholmensis</i>	2	223	239	Balt	Richmondian	Richmondian
55	<i>Trochonema pandori</i>	2	223	239	Balt	Richmondian	Richmondian
56	<i>T. aff. pandori</i>	1	223	239	Balt	Richmondian	Richmondian
57	<i>Lophospira sedgewicki</i>	5	223	273	Laur	Richmondian	Telychian
58	<i>L. ?hyacinthensis</i>	2	223	256	Laur	Richmondian	Richmondian
59	<i>Longstaffia centervillensis</i>	3	257	273	Laur	Rhuddanian	Rhuddanian
60	<i>Arjamannia cancellata</i>	1	257	261	Laur	Rhuddanian	Telychian
61	<i>A. woodlandi</i>	5	257	273	Laur	Rhuddanian	Telychian
62	<i>D. trilineata</i>	3	257	265	Laur	Aeronian	Aeronian
63	<i>Lophospira gotlandica</i>	30	257	337	Laur	Aeronian	Ludfordian
64	<i>Longstaffia laquetta</i>	6	257	301	Laur	Rhuddanian	Homerian
65	<i>A. inexpectans</i>	3	262	273	Laur	Telychian	Telychian
66	<i>Lophospira holmi</i>	1	275	277	Laur	Sheinwoodian	Sheinwoodian
67	<i>Kiviasukkaan nelsonae</i>	1	275	277	Laur	Sheinwoodian	Sheinwoodian
68	<i>Lophospira munda</i>	1	282	294	Laur	Sheinwoodian	Homerian
69	<i>L. imbricata</i>	7	278	330	Laur	Sheinwoodian	Gorstian
70	<i>Eunema turrata</i>	5	278	308	Laur	Sheinwoodian	Homerian
71	<i>E. kayesi</i>	1	282	294	Laur	Sheinwoodian	Gorstian
72	<i>Ruedemannia laevissima</i>	1	295	301	Laur	Homerian	Homerian
73	<i>Arjamannia aulongensis</i>	1	295	301	Laur	Homerian	Whitwellian
74	<i>Ruedemannia robusta</i>	7	282	330	Laur	Homerian	Gorstian
75	<i>Longstaffia tubulosa</i>	3	295	330	Laur	Homerian	Gorstian
76	<i>L. cyclonema</i>	5	302	308	Laur	Homerian	Homerian
77	<i>Trochonema fatua</i>	3	309	330	Laur	Gorstian	Gorstian
78	<i>Loxoplocus soluta</i>	4	309	330	Laur	Gorstian	Gorstian
79	<i>Lophospira cochleata</i>	3	309	330	Laur	Gorstian	Gorstian
80	<i>Trochonema muricata</i>	1	331	332	Laur	Ludfordian	Ludfordian
81	<i>Ruedemannia subrobusta</i>	3	331	337	Gond	Ludfordian	Ludfordian
82	<i>Prychozone aberrans</i>	2	331	337	Gond	Ludfordian	Pridoli

APPENDIX 4

SYSTEMATIC PALEONTOLOGY

In the interest of conserving space, taxonomic revisions are presented only for new genera and for those requiring rediagnoses. Genera merely redefined but retaining traditional diagnoses are reclassified as per Fig. 14.

SUPERFAMILY LOPHOSPIROIDEA NOM. TRANS. WENZ, 1938

FAMILY LOPHOSPIRIDAE WENZ, 1938

Diagnosis: Lophospiroids primitively featuring a trilineate sinus keel, a strong left ramp carina, and a deep sinus that curves back to the sinus keel. All of these features change within the family in at least one subclade.

Included Genera: *Lophospira*, *Donaldiella*, *Loxoplocus*, *Eunema*, *Gyronema*, *Ruedemannia*, *Arjamannia*, *Paupospira* gen. nov., *Frodospira* gen. nov.

Genus *Eunema* Salter, 1859

Diagnosis: Prominent, sharp right and left ramp carina. Strong medial keel usually bordered by peripheral lira (although not in types species). Shallow sinus trending nearly straight into sinus keel. Increasing translation during final whorls, sometimes resulting in disjunct coiling.

Type Species: *Eunema strigillata* Salter, 1859.

Additional Species: "*Lophospira*" *centralis*, "*L.*" *helicteres*, "*L.*" *concinula* Ulrich and Scofield, 1897, "*L.*" *quadrisulcata*.

Discussion. Knight *et al.* (1960) considered *Eunema* to be a polyphyletic subgenus of *Trochonema*, meant to describe high-spired variants of that genus. However, phylogenetic analyses indicate that the synapomorphies of *Eunema* and *Trochonema* are parallelisms. Knight *et al.* (1960) acknowledged the polyphyletic nature of the Trochonematidae by noting that the diagnostic characters (*e. g.* shallow sinus and a medial keel) appeared to be convergent among many forms. This analysis takes their conclusions a step further by positing that the form is polyphyletic among lophospiroids. The much more restrictive definition presented here excludes several species previously assigned to *Eunema*, which have been reassigned to genera such as *Globonema*.

First-known appearance (FKA): "*Lophospira*" *centralis*: Murfreesboro Limestone (Early Caradoc [Ashbyan]).

Last-known appearance (LKA): "*Lophospira*" *quadrisulcata*: Maquoketa Formation (Early Ashgill [Maysvillian]).

Genus *Loxoplocus* Fischer, 1885

Syn. *Kiviasukkaan* Peel, 1975b

Diagnosis: Sharp and strong medial keel that hooks slightly adapically, typically bordered by sharp but much weaker peripheral lira (although seemingly not on the type species). Narrow, shallow sinus,

curving back towards sinus keel. Dull but strong left ramp carina, with right ramp concave and featuring a sharp carina at the suture, which creates an acute sutural margin. Increasing translation during final whorls, sometimes resulting in disjunct coiling (with the type species showing disjunct coiling throughout life).

Type Species: "*Murchisonia*" *soluta* Salter, 1859.

Additional Species: "*Lophospira*" *sedgewicki* Donald, 1906, "*L.*" *?bellicarinata* Donald, 1906, "*L.*" *gotlandica* Ulrich and Scofield, 1897, "*Kiviasukkaan*" *nelsonae* Peel, 1975b.

Discussion: Knight *et al.* (1960) originally defined *Loxoplocus* as a broad genus that included *Lophospira* and other subgenera, an interpretation rejected by more recent authors (*e. g.* Tofel and Bretsky, 1987). It now is restricted to a paraclade of lophospiroids whose most prominent features include increasing translation over ontogeny, a very acute suture, and a very concave right ramp.

FKA: "*Lophospira*" *sedgewicki*: "Starfish Beds," Girvan District (Late Ashgill [Rawtheyan]).

LKA: "*Lophospira*" *gotlandica*: Kopanina Formation (Late Ludlow [Ludfordian]);

Genus *Paupospira* gen. nov.

Fig. 14

Diagnosis: Thick columella, filling the entire umbilicus and producing a shovel-like siphon in extreme cases. Deep and wide sinus curving back strongly to sinus keel. Sinus keel trilineate on early whorls, but with trilineations often vague and weak on adult whorls.

Type Species: *Lophospira oweni* Ulrich and Scofield, 1897.

Additional Species: "*Lophospira*" *burginensis*, "*L.*" *tenuistriata* Ulrich and Scofield, 1897, "*L.*" *summerensis* Ulrich and Scofield, 1897, "*L.*" *tropidophora* Meek, 1873, "*Schizolopha*" *moorei*, "*Donaldiella*" *bowdeni* (Safford, 1869), "*Hormotoma*" *trilineata* Foerste, 1923.

Etymology: For David Swofford's computer program PAUP ("Phylogenetic Analysis Using Parsimony"; Swofford, 1998), which helped to diagnose and define this clade.

Discussion: *Paupospira* matches a monophyletic group originally hypothesized by Ulrich and Scofield (1897). A new genus is erected to recognize that group. The most distinguishing feature is the extremely thick columella, which often preserves as a core without the rest of the shell. Cladistic depictions of relationship highlighting the key features are given in Fig. 14.

FKA: "*Lophospira*" *burginensis*: Leray beds, Rockland

Formation (Middle Caradoc [Rocklandian]).

LKA: "*Hormotoma*" *trilineata*: Saugh Hill Group (Middle Llandovery [Aeronian]).

Genus *Frodospira* gen. nov.

Diagnosis: Very small shells, with strong ornament that leaves imbrications on the growth lines, a strongly adapically curved medial keel, and highly tangential apertures.

Type Species: "*Murchisonia*" *imbricata* Lindström, 1884.

Additional Species: "*Lophospira*" *munda* (Lindström, 1884), "*L.*" *cochleata* (Lindström, 1884).

Etymology: After J. R. R. Tolkien's character from *Lord of the Rings*, reflecting the unusually small size of the known species. Hypotheses about extraneous epididial tentacles are purely speculative.

Discussion: This closely matches Ulrich and Scofield (1897: 963) *imbricata* subsection of *Lophospira*. The genus is remarkable in that all known species are known only from very small shells. As these shells are found in the same assemblages as large gastropods, it appears to represent a character of the genus rather than a taphonomic artifact. The illustrations of these species, provided by Lindström (1884) are very accurate and convey the general characters very well.

FKA: "*Lophospira*" *munda*: C beds, Visby Formation (Early Wenlock [Sheinwoodian]).

LKA: "*Lophospira*" *imbricata*: Upper Hemse Beds (Early Ludlow [Gorstian]).

FAMILY TROCHONEMATIDAE ULRICH AND SCOFIELD, 1897

Diagnosis: Trochiform, widely umbilicate lophospiroids. Early forms retain wide, and deep sinus curving back to a trilineate selenizone, but later forms possess either the medial lira only or the peripheral lira only. Sharp left and right ramp carina with strong umbilical and sutural carina found on most species.

Included Genera: *Trochonemella*, *Trochonema*, *Globonema*.

Discussion: Knight *et al.*'s (1960) reduction of the Trochonematidae is advanced here. Preliminary analyses (Wagner, unpub. data) indicate that Devonian genera assigned to the Trochonematidae such as *Trochonemopsis* belong to the Euomphalinae. At this time, it is not clear if any post-Silurian genera assigned to this family belong here.